# THE EVOLUTIONARY ECOLOGY OF ELEVATIONAL SPECIALIZATION IN TROPICAL MONTANE BIRDS

A Dissertation

Presented to the Faculty of the Graduate School

of Cornell University

In Partial Fulfillment of the Requirements for the Degree of

Doctor of Philosophy

by

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February 2016

# THE EVOLUTIONARY ECOLOGY OF ELEVATIONAL SPECIALIZATION IN TROPICAL MONTANE BIRDS

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Cornell University 2016

Tropical mountains are the most biodiverse terrestrial systems on Earth. This "megadiversity" is largely because tropical montane species inhabit narrow elevational distributions—understanding why tropical mountains are so biodiverse thus requires understanding the factors that explain elevational specialization. In my dissertation, I explored the role of two factors previously hypothesized to explain why tropical birds inhabit narrow elevational zones—temperature and interspecific competition. In Chapter 1, I describe resurveys of New Guinean montane bird communities originally surveyed by Jared Diamond in the 1960s, and demonstrate rapid warming-associated upslope shifts in these avifaunas. In Chapter 2, I test the hypothesis that these recent upslope shifts are the result of thermal specialization in New Guinean montane birds. However, I find no evidence that species' exhibit local adaptation to ambient temperature in their thermal physiology (lower critical temperatures and thermal conductances), suggesting New Guinean montane birds' elevational limits are minimally influenced by thermal specialization. I then use a comparative approach in Chapter 3 to test whether species exhibit local adaptation to cold high elevation environments in body size, and find little evidence that body size clines are positively linked to elevation in both intraspecific and interspecific analyses. These analyses suggest that temperature may primarily exert an indirect influence on tropical birds' elevational distributions (e.g., by altering biotic interactions with prey, predators or

competitors). One biotic interaction hypothesized to be important in tropical montane avifaunas is interspecific competition, which has been argued to explain why a common pattern is for closely related species to inhabit different elevational zones in a “layer cake” pattern. In Chapter 4, I find broad support for a model of community assembly wherein competitive interactions upon secondary contact drive elevational divergence between sister species of tropical montane birds. I move from evolutionary pattern to ecological process in Chapter 5, where I test the hypothesis that interference competition is a mechanism limiting species’ elevational distributions. Playback experiments in five species-pairs of New Guinean songbirds with “layer cake” patterns revealed strong interspecific aggression in all cases where species-pairs interact with their putative competitors, providing experimental data consistent with the hypothesis that interspecific competition is a factor limiting these species’ elevational distributions.

## BIOGRAPHICAL SKETCH

Benjamin Freeman's first memory is of watching a flock of American White Pelicans floating overhead in the Eastern Washington desert. Since this fateful moment, wild landscapes and the avian creatures that dwell in them have exercised a strong grip on Ben's imagination.

Born in Baraboo, Wisconsin, Ben grew up in Seattle, Washington, and developed an affinity for the dark misty forests of the Pacific Northwest. Family camping trips (with father Scott, mother Susan and brother Peter Freeman) nurtured his appreciation for poking sea anemones and chasing after butterflies, but fragments of youthful journals and family recollections both attest to the often central importance of finding, identifying, and watching birds to Ben's developing psyche during this era. For example, he once prevailed upon his dutiful father to type out lists of the birds found in different states in advance of a cross-country family trip, presaging Ben's future academic interests in distributional ecology.

Ben's teenage years were devoted to playing soccer, actively participating in his high school's phenomenal outdoor education program, and writing for his high school newspaper. Though Ben seldom toted binoculars during these years, he undertook his first efforts to engage his peers in the wonders of ornithology by testing high school freshmen on their ability to correctly distinguish dried bird poop on a rock from blobs of white toothpaste carefully placed in mimetic fashion nearby. Watching his charges use sight, smell and taste to attempt to solve this surprisingly difficult riddle gave Ben his first lesson in pedagogy; there is no substitute for reasoned trial and error—the scientific method—, and science is best learned by *doing*.

Ben completed his college years in St. Paul, Minnesota, where he attended Macalester College. Drawn to Macalester by its excellence in the liberal arts, urban location and creative student body (sample cheer: "Drink blood! Smoke crack! Worship Satan! Go Mac!"), he initially

planned to major in geography with an emphasis on urban planning. However, simultaneous field projects in ecology and urban geography completed during his first fall, completed with markedly different levels of success, led to Ben shifting his interest squarely onto the biological sciences, a decision that appears obvious in retrospect. He quickly took all the organismal biology courses on offer, and even ventured outside the liberal arts cocoon to enroll in an upper division animal behavior course at the nearby University of Minnesota.

The defining experience of Ben's college career came when he left school for a semester in order to work as a field assistant studying avian austral migration on a remote Bolivian cattle ranch. In addition to learning standard field ornithology methods, Ben was overwhelmed by the phenomenal biological diversity on display. He recalls spending hot afternoons poring through thick field guides in the often-vain attempt to identify confusingly similar species, learning colorful slang from an Argentine colleague, and celebrating his 21$^{st}$ birthday by eating one of the household chickens as a change of pace from the normal thrice-daily meals of rice and beef jerky. Upon returning stateside, Ben hatched plans to return to the Neotropics after graduating, and he spent nearly the entire year of 2007 in South America. He worked as a birding guide in Brazil, visited newly created reserves in Colombia, and studied cloud forest birds in Ecuador, where he learned that an aspiring biologist could achieve (limited) fame and glory by describing nests, eggs, and parental care of poorly studied Andean species. It was during this time that Ben met his future wife, Alexandra Class, then conducting her dissertation research in Ecuador, impressing her with his recent discovery of an active Sharpe's Wren nest. Ben's passion for natural history continued during stints guiding birding tours in Colombia in the ensuing years, during which time he learned firsthand the distributional ecology of the Andean avifauna.

Ben's transition from "freelance bird guide / natural history enthusiast" to the rarefied corridors of academia was, in his recollection, difficult. He was accepted in the Department of Ecology and Evolutionary Biology at Cornell to the lab of Dr. John Fitzpatrick (aka the entire Lab of Ornithology) and leapt into the world of graduate school despite missing the annual Cornell EEB invited students weekend (he was guiding clients around remote Colombian mountains at the time). Ben found graduate school overwhelming at first, and feared that he would forever feel out of his depth. Yet with time, support from Fitz and other faculty advisors and new friends, he found his footing and embarked on a series of research projects that proved fruitful. Ben was fortunate to enmesh himself in the Lab of Ornithology community, learning to record birds with the Macaulay Library, getting hooked on eBird (and its research applications) from the eBird project leaders themselves, and, to his family's amusement, generally being surrounded by folks more knowledgeable than he in avian matters. Now headed to a postdoctoral position working with Dr. Dolph Schluter at the University of British Columbia, Ben leaves Cornell a married man, a father, and a better human being than when he arrived.

To my grandfather A. Carl Leopold, for marrying a gentle demeanor with a fierce devotion to doing what is right; you demonstrated what a good life looks like.

## ACKNOWLEDGMENTS

I did not become a biologist to toil in isolation, and gratefully acknowledge the assistance of a small army of advisors, colleagues, friends and family. To my advisor, Dr. John Fitzpatrick, who shepherded me into this project and provided feedback and support at critical junctures while trusting me that following my (research) bliss would lead to positive outcomes. Fitz provides a model example of what a successful conservationist looks like, meshing his passions for research with a commitment to spreading the gospel that our lives are richer when we are surrounded by biodiversity and pay attention to the lives of our avian neighbors. I hope to follow his example as I embark on my career. To Dr. Irby Lovette, who welcomed me into his lab group upon my arrival at Cornell, saw promise in early drafts of sprawling manuscripts, and helped make my dream of teaching an undergraduate field course a reality. To Dr. Anurag Agrawal, the final member of my committee, for his cheerful demeanor and ability to identify the core biological problem under discussion and how to go about studying it—an exceptionally clear scientific thinker. Many other faculty members provided support, shared field stories, and generally helped me develop as a scientist; Drs. Andre Dhondt, Kelly Zamudio, Harry Greene, Amanda Rodewald, David Winkler, Bob Ricklefs (at University of Missouri St. Louis) and particularly to Dr. Monica Geber, whose compassion and empathy made all the difference.

The prospect of joining Fitz's lab—the entire Lab of Ornithology—was a major draw when I elected to pursue graduate studies at Cornell. I am grateful for the opportunity to be part of the Lab of O community, and have benefited enormously from this experience. To Dr. Wes Hochachka, who generously shared his statistical acumen and good cheer. To Matt Medler, Greg Budney, Martha Fischer and Jay McGowan at the Macaulay Library, who provided the equipment and know-how to conduct playback experiments in the field. To Dr. Frank La Sorte,

for helping solve analytic puzzles and introducing me to species distribution modeling. And to staff at the Lab of O—Melissa Walker, Cindy Marquis, Zhila Sadri and Karen Ingall—and in Corson-Mudd—Patty Jordan, Carol Damm, and Dawn Potter—for helping me cross my administrative "t's" and dot my bureaucratic "i's."

I am fortunate to have spent big chunks of my graduate career in Ithaca, and am pleased to thank the wide array of friends (colleagues!) who have helped me grow as a biologist and person. To, in no particular order, Nathan Senner, Nancy Chen, Yula Kapetanakos, Shane Peace, Kevin Loope, Gui Becker, Monica Kersch Becker, Chris Dalton, Rayna Bell, Marjorie Weber, Katie Wagner, Amos Belmaker, Nick Bruns, Sara Keen, Ezra Lencer, Nick Mason, Leo Campagna, Scott Taylor, Sahas Barve, Eliot Miller, Matt Lewis, Jake Berv, Bret Pasch, Emma Grieg, Dave Toews, Vanya Rohwer, Chris Wood, Jessie Barry, Marshall Iliff, and many many others. Special thanks to those of you who showed me the friendship and support that helped me slowly recover after devastating events. In fieldwork, to Dr. Bruce Beehler, Jen Mandeville, John Anuabo and a long list of local landowners and field assistants in Karimui and the YUS Conservation Area; from the bottom of my heart, to Ness Martin, Dr. Tanya Ihle, Dame Carol Kidu, Sir Peter Barter, Paki Toko, Peter Navratil and Vicki and Brett Middleton for assisting us in our darkest hour.

I was given the opportunity to develop and teach an international field course in my penultimate semester at Cornell; to John Fitzpatrick, and particularly, Irby Lovette, for providing me this opportunity. Teaching *Advanced Tropical Field Ornithology* provided me with structure at a challenging time in my life and I was inspired by the students whose hard work and cheerful dispositions uplifted my spirits—to Teresa Pegan, Reid Rumelt, Taylor Lynn Heaton Crisologo,

Mary Margaret Ferraro, Nathaniel Young, Lauren Flesher, Eric Sibbald, Eric Gulson and Sarah Dzielski.

Throughout my life, I have leaned on my family for support, guidance and encouragement. It is a gift to have grown up spending weekends and school breaks exploring forests, mountains and coastlines; not all children receive such a splendid education in the outdoors. To Carl and Lynn Leopold, my lovely grandfather and step-grandmother and the reason I visited Ithaca growing up. I was so looking forward to spending years living next door to both of you. This was not to be. Yet it has been our tremendous good fortune to visit Lynn at the Woodlot every couple weeks for waffles and wine, to split firewood and admire night-blooming *Cereus*. We miss you Carl. To my talented brother Peter: you are a thoughtful man who can also make me giggle uncontrollably; it has been a pleasure to see you come into your own over the past couple years. To my parents, Scott and Susan. A laundry list of all the ways you are important would overwhelm even this long dissertation; you are great. I love you very much. To Alexa, my lovely wife. We have traversed the world together, seen beautiful things and experienced some of the ugliest. We have held tight to one another throughout, and our tight bond has made all the difference. You have my complete love and admiration. And to Felix, our dear infant son. Your smiles and laughs are the sweetest medicine; I can't wait to see you grow and develop into your own person as the years unfold.

Last, to the agencies and foundations that provided the research grants that supported my fieldwork and studies. To the National Science Foundation, who awarded me a pre-doctoral fellowship that gave me the time to think broadly and travel widely. Any opinions, findings, and conclusions or recommendations expressed in this material are those of the author and do not necessarily reflect the views of the National Science Foundation. To the Kieckhefer Adirondacks

Fellowship, AMNH Collection Study Grant, Explorer's Fund, and Atkinson Center Sustainable Biodiversity Fund, for invaluable support. And to the Athena Fund of the Cornell Lab of Ornithology, which provided repeated support that enabled our climate change resurveys, and to Mychelle Panzer, who reminds me to pause during my research and simply enjoy life on an aesthetic level.

## TABLE OF CONTENTS

## LIST OF FIGURES

## LIST OF TABLES

CHAPTER 1

# RAPID UPSLOPE SHIFTS IN NEW GUINEAN BIRDS ILLUSTRATE STRONG DISTRIBUTIONAL RESPONSES OF TROPICAL MONTANE SPECIES TO GLOBAL WARMING

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## ABSTRACT

Temperate zone species have responded to warming temperatures by shifting their distributions poleward and upslope. Thermal tolerance data suggests that tropical species may respond to warming temperatures even more strongly than temperate zone species, but this prediction has yet to be tested. We addressed this data gap by conducting resurveys to measure distributional responses to temperature increases in the elevational limits of the avifaunas of two geographically and faunally independent New Guinean mountains, Mt. Karimui and Karkar Island, 47 and 44 years after originally surveyed. Though species richness is roughly five times greater on mainland Mt. Karimui than oceanic Karkar Island, distributional shifts at both sites were similar: Upslope shifts averaged 113 m (Mt. Karimui) and 152 m (Karkar Island) for upper limits and 95 m (Mt. Karimui) and 123 m (Karkar Island) for lower limits. We incorporated these

results into a meta-analysis to compare distributional responses of tropical species to those of temperate zone species, finding that average upslope shifts in tropical montane species match local temperature increases significantly more closely than in temperate zone montane species. That tropical species appear to be strong responders has global conservation implications and provides empirical support to hitherto untested models that predict widespread extinctions in upper-elevation tropical endemics with small ranges.

## INTRODUCTION

Temperate species are responding to anthropogenic temperature increases by rapidly shifting geographic distributions to track their climatic niche (1-3). These shifts appear to be increasing in pace – a recent meta-analysis concluded that species are shifting their distributions pole-ward and upslope much faster than previously estimated (1, 2). Range shifts are less studied in tropical regions however (1, 4, 5), despite being home to the vast majority of biodiversity (6). Notwithstanding strong latitudinal bias in empirical studies, climate change-driven range shifts are predicted to cause widespread extinctions in both temperate and tropical species within the next century (7-10).

With scarce empirical data, models of tropical species' response to temperature increases predict a wide range of responses (11). At one extreme, tropical species may be relatively unaffected, as the magnitude of temperature increases is relatively low in the tropics (12). Alternately, vulnerability to warming temperatures could be highest in the tropics if tropical species are physiological specialized to narrow thermal niches (13-18). Such thermal specialization has been documented in tropical ectotherms (16, 17), but it is unclear whether similar patterns may apply to tropical endotherms, whose distributional shifts in response to warming may result from indirect rather than direct impacts of temperature increases (5).

We resurveyed geographically and faunally independent elevational gradients in New Guinea nearly a half century after they were first surveyed. The original transect surveys were conducted by Jared Diamond to determine bird species' elevational limits on Mt. Karimui (July-August 1965; 19) and Karkar Island (May 1969; 20). These environments differ significantly: Mt. Karimui is located in New Guinea's biodiverse Central Ranges and harbors a diverse resident avifauna of *ca*. 250 resident landbirds (19), while Karkar Island is a small oceanic island off New Guinea's north coast with a depauperate flora and fauna (*ca.* 50 resident landbirds) dominated by highly dispersive taxa (20; Fig 1).

We used elevational limits measured during historical transects and modern resurveys to investigate New Guinean montane birds' response to warming temperatures. We predicted that species have moved upslope relative to historical range limits. Given that tropical species are hypothesized to be especially sensitive to temperature increases (either directly or via indirect ecological interactions), we additionally predicted that the magnitude of upslope shifts would closely match predicted shifts based on local temperature increases. We simultaneously tested two additional hypotheses, investigating whether upslope shifts at the leading range margin outpaced upslope shifts at the trailing range edge (21), and whether species' dietary preferences influenced upslope shifts (22, 23). We then used our data and further recent tropical resurveys to test the "tropical species are strong responders" hypothesis, predicting that upslope shifts measured in tropical resurveys match predicted upslope shifts significantly more closely than for temperate zone resurveys.

## METHODS

**Resurveys.** Our resurveys closely followed Diamond's original methodology (19, 20) and were conducted "blind", without prior knowledge of species' elevational limits measured in Diamond's historical surveys. We used a barometric altimeter (Garmin GPS 62S, accuracy within forest ~ ± 5-8 m in horizontal position) to measure elevation, averaging readings taken on multiple days. Readings taken at the same locality on different days typically varied to a relatively minor degree (e.g., the standard deviation for readings measured on 16 different days at our second camp was 8.6 m). Like Diamond, we calibrated our altimeter for Mt. Karimui at the Karimui airstrip (1,112 m) and on Karkar Island at sea level.

We recorded species' elevational limits as the most extreme elevational observation of a given species. However, we followed Diamond (19, 20) in discounting single observations of common species well above or below their typical elevational distribution. We considered single observations more than 300 m in elevation above or below the next most extreme records to represent outlier observations. Such outlier observations were rare, with only four examples from Mt. Karimui and none from Karkar Island. Including all records, including outlier observations, does not change any results of this study. Finally, we recorded elevational limits only for species where limits fell within the elevational expanse surveyed at our study sites.

**Mt. Karimui.** Mt. Karimui is an extinct volcano in New Guinea's Central Ranges, in Chimbu Province (Fig 1). In July-August 1965, Diamond surveyed the avifauna of Mt. Karimui's northwestern ridge from *ca*. 1,100 m to the summit at 2,520 m (19). We conducted a modern resurvey in June-July 2012, studying the same ridgeline at the same time of year. We confirmed the exact ridge studied by Diamond by personal communication with J. Diamond and interviewing Karimui residents, including a village elder who had participated in the 1965

expedition. Mt. Karimui was entirely covered in primary forest in 1965, and land-use changes in the intervening decades have been minimal. Small-scale forest clearance for subsistence agriculture is limited to elevations below 1,275 m, with the exception of a small (*ca.* 1 ha) patch atop the ridge's summit cleared during recent construction of a cell phone tower. We avoided sampling in the vicinity of subsistence gardens by surveying lower elevations (from 1,130 to 1,330 m) on an undisturbed forested ridge 0.5 km to the east. We then surveyed Diamond's exact transect on Mt. Karimui's northwest ridge from 1,330 m to the summit at 2,520 m.

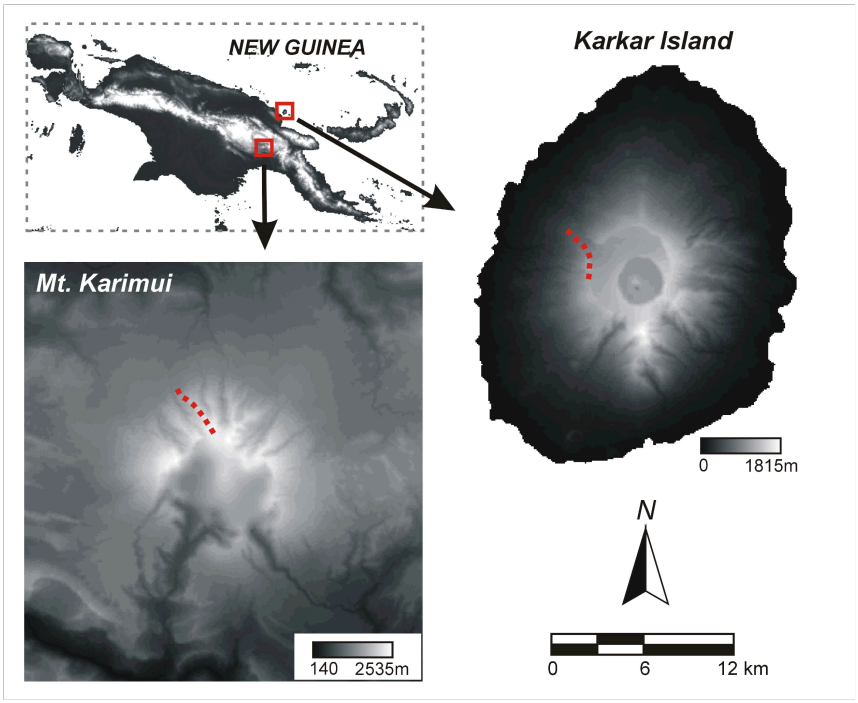


**Figure 1**. Map of resurvey sites in Papua New Guinea. The elevational transects recently revisited by the authors are marked in red (Mt. Karimui: 1,130 m – 2,520 m, Karkar Island: 800 m – 1600 m). Mt. Karimui is an extinct volcano in the southern Central Ranges of New Guinea, while Karkar Island is an oceanic island located 10 miles from the New Guinean mainland. These elevational gradients were originally surveyed by Jared Diamond in the 1960s (Mt. Karimui: 1965, Karkar Island: 1969), and remain covered in primary forest.

Diamond used extensive mist-netting, specimen collection, audial censuses, and ad lib observations to determine species' distributional limits, spending a total of 33 field days on Mt. Karimui (19). We attempted to replicate this field effort, completing extensive mist-netting, point counts, and collecting ad lib observations in 38 field days. We used flagging tape to mark elevational zones every 25 m of elevation, providing a consistent basis for measuring elevation. We then conducted mist-net censuses from 1,130 m to 2,420 m with consistent effort across elevation, opening mist nets at each elevational zone for two mornings (0600 h– 1230 h). Difficult terrain led to reduced mist-net effort in the short (canopy < 15 m), heavily mossed ridgeline forest above 2,250 m and entirely prevented mist-netting above 2,400 m. This reduction in mist-net effort above 2,250 m increased the probability of overlooking species present near the ridge's summit. Because the preponderance of species' range borders near the summit were upper limits (not lower limits), these potential omissions likely reduced our ability to detect upslope shifts in the upper limits of montane birds. Hence, this methodological bias constrained our ability to document upslope shifts of montane species and is conservative with respect to the hypothesis that warming temperatures have led to upslope shifts.

Point counts were conducted by one observer (BGF) with good working knowledge of New Guinean bird vocalizations. A total of 40 point counts were conducted along the elevational gradient (1,130 m to 2,520 m). Points were separated by at least 150 m, with each point count site visited on three mornings (0630 h to 1200 h) for five minutes per count. A second set of point counts was completed in our second Mt. Karimui resurvey in October-November 2012. This independent Mt. Karimui resurvey covered elevations from 1,330 m to 2,520 m, and used point count data and ad lib observations compiled during 34 days of fieldwork. Point counts were

completed at 30 sites from 1,330 m to 2,520 m in this second Mt. Karimui resurvey following the methodology described above.

**Karkar Island.** Our second resurvey took place on Karkar Island, Madang Province, an oceanic island located ten miles off the coast of northern New Guinea (Fig 1). An active volcano, Karkar's forested slopes rise to a steep-sided caldera at 1,300-1,400 m in the island's center. The island's high point, at *ca.* 1,800 m, is Mt. Kanagioi, at the southern rim of the caldera. Jared Diamond surveyed Karkar Island's upland (> *ca*. 400 m) avifauna in May 1969. We conducted our resurvey of Karkar Island's montane avifauna in April 2013, at the same time of year and visiting the same locations as Diamond's original transect. However, because plantation agriculture currently extends to around 600 m on Karkar Island, we restricted our resurvey to undisturbed montane forest from 800 m to 1,600 m. Diamond used mist-netting, audial censuses, and shotgun-based collecting to document elevational limits of species on the northwest side of the island, spending nine field days in Karkar's montane forests (20). We expended similar field effort, gathering distributional data over ten days of mist-netting, conducting point counts (35 sites, methods described above), and collecting ad lib observations.

**Statistical analysis.** We used parametric and non-parametric t-tests and sign tests to evaluate upslope shifts. One sample t-tests tested the significance of upslope shifts at both upper and lower limits for both Mt. Karimui and Karkar Island. Sign tests compared the number of upslope to downslope shifts at both upper and lower limits. Two-sample t-tests compared the magnitude of upslope shifts between study sites. Because changes in elevational limits measured on Mt. Karimui in June-July and October-November were not normally distributed, we used Wilcoxon

signed-rank tests to test for systematic biases in the seasonality of elevational limits. We used paired t-tests for two comparisons of Mt. Karimui species, limiting our database to species where both upper and lower limits were measured ($N$= 41 species). First, we tested whether the magnitude of upslope shift differed between upper and lower limits. Second, we tested whether species expanded their elevational breadth between Diamond's original transect and our resurvey.

To consider the possibility that estimated changes in elevational distributions were influenced by species' relative abundance during our modern resurvey, we compared species' detectability to estimated shifts at both upper and lower elevational limits. Specifically, we used linear regression models to test the influence of species' relative detectability (summed number of times a species was detected on point counts and captured in mist nets) on upper and lower limit distributional shifts. We also investigated whether diet impacted species' upslope movement. First, we used reference material (19, 32) to classify species into five dietary guilds: carnivores, frugivores, insectivores, omnivores and nectivores. We then used ANOVAs to test for differences in species' upslope movements between foraging guilds, testing both range margins on Mt. Karimui and upper limits on Karkar Island.

Finally, we estimated change in average temperature for our study sites using the 0.5 x 0.5 degree grid cells containing our study sites within the CRU TS 3.2 database (25). Specifically, we compared mean annual temperatures for the decade prior to the historical transect (Mt. Karimui: 1955-1964, Karkar Island: 1959-1968) to the decade prior to our modern resurveys (2002-2011). We measured the lapse rate on Mt. Karimui by placing temperature loggers along the elevational gradient and regressing mean daily temperature against elevation.

**Tropical vs. temperate zone resurveys.** We analyzed the rate of upslope shifts between temperate and tropical regions by summarizing observed and expected shifts from 35 resurveys. Specifically, we added novel data (our two resurveys and three further recent tropical resurveys; 5, 26, 27) to the database originally presented in Table S1b by Chen et al. (1). We followed Chen et al.'s methodology (1) in adding recent resurveys measuring distributional responses to warming temperatures. For example, we did not treat upslope shifts at leading and trailing range margins measured on Mt. Karimui and Karkar Island as independent. Instead, we included each site as a single resurvey, summarizing upslope shifts using weighted means based on the number of species in each group (upper and lower limit shifts) at each study site. Additionally, for novel resurveys, we used observed and expected elevational shifts reported in the original studies. We note the following caveats to our meta-analysis: published tropical resurveys are still few, diverse in taxa studied (e.g., trees, plants, birds, lizards and moths) and vary in scope (e.g. elevational shifts in one study (27) were presented at the genus, rather than species, level).

To investigate hypothesized differences between responses in tropical and temperate biotas, we first categorized resurveys as either tropical (occurring between the Tropics of Cancer and Capricorn) or temperate (occurring pole-ward of the tropical zone). We categorized the recent resurvey of montane Taiwanese plants (26) as tropical, as Taiwan is located almost exactly on the Tropic of Cancer. We then calculated shift rates (observed shift/predicted shift based on temperature increase) for each resurvey, and compared shift rates between tropical and temperate zone species using a two-sample t-test.

## RESULTS AND DISCUSSION

Land-use changes along the elevational gradients studied on Mt. Karimui and Karkar Island have been minimal: Climate change is the only major environmental change that has occurred since Diamond's historical transects (24). Long-term temperature data from our study sites does not exist, so we used global climate models to estimate the magnitude of warming in the 0.5 x 0.5 degree grids containing our study sites (25), following the methodology of similar resurveys (1, 4, 5). These models estimated an increase in annual mean temperature of $0.39^0$C and $0.46^0$C between historical transect and modern resurvey for the grid cells containing Mt. Karimui and Karkar Island, respectively (25). Average temperature declines linearly with elevation on tropical mountains, and we measured the lapse rate on Mt. Karimui as $0.51^0$C per 100 m. Applying this lapse rate to estimated temperature increases predicted elevational shifts of 76 m for Mt. Karimui and 90 m for Karkar Island.

We resurveyed identical transect locations at the same time of year (Mt. Karimui: June-July 2012, Karkar Island: April 2013), and with similar survey effort to Diamond's historical surveys (see additional methods). We also conducted a second resurvey of Mt. Karimui in October-November 2012 to test whether seasonal variation affected avian elevational distributions. Although separated by only a few months, these two modern resurveys represent distinct seasons for birds in the New Guinea highlands – June-July is the peak of the dry season and after the end of the main breeding season, while October-November approaches the peak of the rainy season and is the beginning of the breeding season (19). There was no systematic bias in elevational limits measured on Mt. Karimui in October-November 2012 compared to limits measured in June-July 2012 for either upper ($N$= 96; 19 ± 163 m; Wilcoxon signed-rank V= 1196, $P$= 0.23; all statistics presented are mean ± sd) or lower limits ($N$= 36; 13 ± 148 m; Wilcoxon signed-rank V= 316, $P$= 0.79). We therefore present the results of analyses using June-

July data in this manuscript, as this resurvey closely matches the seasonality of the historical survey conducted in July-August.

Bird species significantly shifted their upper limits upslope on both Mt. Karimui (113 ± 197 m; $N$= 123; $t_{122}$= 6.30, $P$ < 0.001) and Karkar Island (153 ± 184 m; $N$= 22; $t_{21}$= 3.90, $P$ < 0.001; Fig 2). Upslope shifts also occurred at species' lower limits on Mt. Karimui (95 ± 190 m; $N$= 53 species; $t_{52}$= 3.63, $P$ < 0.001; Fig 2). Few species are restricted to montane elevations on Karkar Island. Consequently, upslope shifts in species' lower limits at this site were not statistically significant (123 ± 200 m; $N$= 5 species; $t_4$= 1.38, $P$= 0.24), and we do not further consider shifts at lower limits on Karkar Island. Upslope shifts significantly outnumbered downslope shifts at both upper (Mt. Karimui: 87 upslope, 36 downslope, $P$ < 0.001; Karkar Island: 17 upslope, 5 downslope, $P$= 0.017) and lower limits (Mt. Karimui: 39 upslope, 14 downslope, $P$ < 0.001, Fig 2). Because species on Mt. Karimui moved upslope at both upper and lower limits, the total elevational extent of species' elevational distributions did not change ($N$= 41; paired t-test: $t_{40}$= -0.82, $P$= 0.42). Finally, average upslope shifts exceeded predicted shifts based on estimated warming in all cases, though we caution that global temperature models may not precisely estimate local temperature increases and note the wide variation in measured upslope shifts.

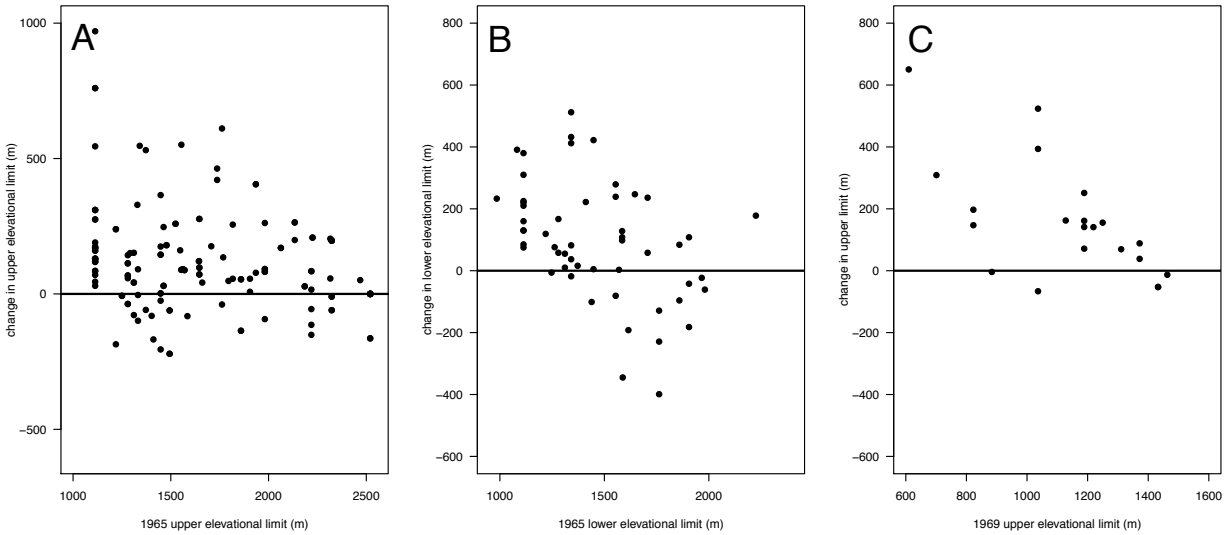


**Figure 2**. Changes in species' elevational limits for (**A**) Mt. Karimui upper elevational limits, (**B**) Mt. Karimui lower elevational limits and (**C**) Karkar Island upper elevational limits. Changes in species' elevational limits between historical and modern resurveys are plotted against historical elevational limits measured in the 1960s. Points on the solid zero-change lines represent species with unchanged elevational limits.

Upper limit range shifts were greater than lower limit range shifts at both study sites, but this difference was not significant (Mt. Karimui, $N$= 41; paired t-test: $t_{40}$= 0.82, $P$= 0.42). Variation in species' responses was weakly influenced by diet on Karkar Island (upper limit: $F_5$= 2.6, $P$= 0.066) but not on Mt. Karimui (upper limit: $F_4$= 0.64, $P$= 0.63; lower limit: $F_3$= 1.53, $P$= 0.22). Specifically, upslope shifts in Karkar Island species' upper limits were larger for omnivores ($N$= 3: 330 ± 289 m) and frugivores ($N$= 7: 242 ± 178 m) than for insectivores ($N$= 5: 107 ± 181 m) and nectivores ($N$= 3: 88 ± 60 m).

A recent meta-analysis found that elevational shifts documented in 31 resurveys comprising a variety of taxa averaged less than half of predicted shifts based on local temperature increases (1). That analysis, however, contained only two resurveys from tropical regions, and therefore

did not compare upslope shifts between tropical and temperate species. Our two resurveys, in conjunction with further recent tropical resurveys across a variety of taxonomic groups (5, 26, 27), provide sufficient tropical data points to permit such a statistical comparison. We used shift rate (observed shift/expected shift given local temperature increase) to summarize upslope shifts, where lag times in upslope shifts are represented by shift rates less than 1. Tropical species' upslope shifts closely matched predicted shifts, with shift rates significantly greater than temperate zone species (tropics: 0.97 ± 0.55, $N$= 7; temperate zone: 0.33 ± 0.29, $N$= 28; $t_{5.6}$= -3.1, $P$= 0.021; Fig 3). Though the number of tropical resurveys conducted is still small, this result supports the hypothesis that tropical montane species are more sensitive to changes in annual mean temperature than temperate zone montane species.

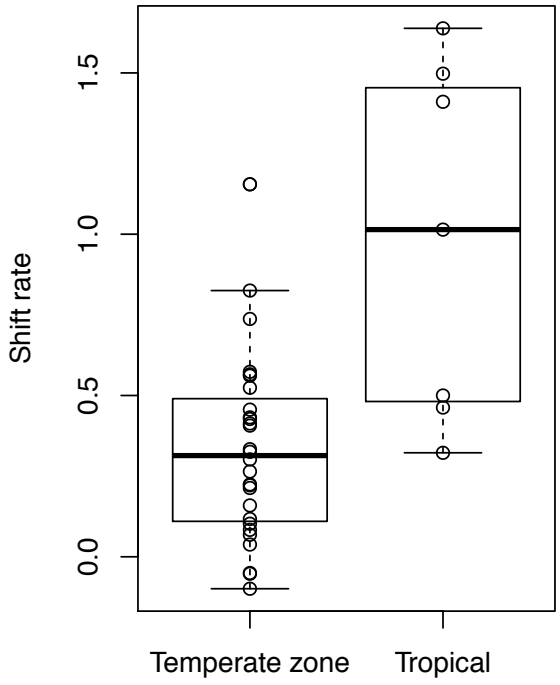


**Figure 3.** Shift rates of temperate zone and tropical montane organisms in resurveys documenting distributional responses to temperature increases. Shift rates represent the average upslope shift (m) documented in a resurvey compared to the predicted upslope shift (m) given local temperature increase. A shift rate of 1 signifies observed shifts that match predicted shifts. Boxplots with median and quartile values for temperate zone and tropical shift rates are overlain on points summarizing shift rates of temperate zone ($N$= 28) and tropical ($N$= 7) resurveys of a variety of taxonomic groups.

Comparing single resurveys to historical data may be confounded by seasonal variation in elevational distributions (5). However, modern elevational limits were not systematically biased upslope or downslope between dry and wet seasons on Mt. Karimui, suggesting the upslope shifts we report are robust to seasonal variation in elevational limits. A second problem affecting resurveys is accounting for differences in survey methodology (28). Comparison of modern and historical (19, 20) databases and methods (see expanded methods) suggests that our methodologies and survey efforts for both Mt. Karimui and Karkar Island were similar, and our data support this contention. In particular, if modern and historical surveys differed in observer ability or effort, the survey with the greater effort should tend to yield broader elevational ranges merely owing to increased sample sizes. Instead, we found that species generally shifted upslope at both upper and lower range limits, as predicted for responses to warming temperatures. Lastly, we note that readily-detected species did not demonstrate stronger upslope shifts: the magnitude of estimated distributional shifts was unrelated to relative detectability at both upper ($F_{1,136}$= 2.40, $P$= 0.12, adj. $r^2$= 0.010) and lower limits ($F_{1,52}$= 1.70, $P$= 0.20, adj. $r^2$= 0.013, see additional methods).

Substantial variation existed among species in observed upslope shifts (Fig 2), typical for such resurveys (1, 22). This variation may arise from idiosyncratic, species-specific responses to either temperature itself or altered resource availability, habitat structure, competitive dynamics, disease prevalence and/or predation associated with increased temperature at given elevations. Ecological traits associated with dietary breadth have been hypothesized to explain variation in species' responses (5, 22). We found no correlation between diet and range shifts on Mt. Karimui. However, upslope shifts were largest in omnivores and frugivores in the depauperate

avifauna of Karkar Island, providing some support for the hypothesis that dietary breadth (omnivores) and patchiness of resource supply (frugivores) may predispose species to stronger distributional responses to increases in mean annual temperature. We conclude that the mechanisms driving upslope shifts in New Guinean birds remain largely uncertain and merit further experimental investigation.

New Guinean birds have responded to a half-century of warming temperatures by rapidly shifting their distributions upslope. Temperatures in New Guinea are predicted to increase $2.5^0$C by 2100 (24). Extrapolating from documented shifts suggests New Guinean birds will respond to rising temperatures by shifting as much as 500 m further upslope by 2100. These shifts are likely to cause at least four local 'mountaintop' extinctions on Mt. Karimui and two on Karkar Island. For example, the montane White-winged Robin's (*Penoethello sigillatus*) lower elevational limit on Mt. Karimui has moved upslope over 100 m since 1965. This species is now found only above 2,330 m on the steep slopes near Mt. Karimui's summit (at 2,520 m), while Mountain Gerygone (*Gerygone cinerea*), Crested Satinbird (*Cnemophilus macgregorii*) and Crested Berrypecker (*Paramythia montium*) are currently restricted to the immediate vicinity of Mt. Karimui's summit. A further ~ $1^0$C temperature increase would likely lead to the extirpation of all four species on Mt. Karimui, though populations will persist on taller mountains elsewhere in New Guinea.

Resurveys to document distributional responses to temperature increase have now been performed in enough different regions to support the hypothesis that tropical montane species are – compared to temperate species – disproportionately sensitive to warming temperatures. Tropical species' sensitivity to temperature may be a consequence of the relative constancy of thermal environments in tropical environments (13, 14), though it remains unclear whether

tropical endotherms' sensitivity to temperature results from indirect ecological interactions or the direct impact of increased temperature (5, 19).

This finding has global conservation implications, as elevational gradients on tropical mountains harbor the most spectacular concentrations of biodiversity of any terrestrial environment (29). In particular, our findings provide empirical support for models that predict widespread extinctions of tropical birds due to temperature increases (8, 10), with global extinctions especially likely in tropical species endemic to single mountains or small mountain ranges (10, 18). Further, we emphasize that species upslope shifts on Mt. Karimui have not resulted in expanded elevational distributions. Instead, species' entire elevational distributions are shifting upwards. Because less land area typically exists at higher elevations (15), upslope shifts in response to warming temperatures will inexorably cause reductions in species' populations, increasing the probability that these diminished populations will go extinct (30).

Conservation of tropical montane biotas in the face of warming temperatures clearly will require protection of entire elevational gradients (31). While species appear likely to shift their distributions upslope, intact elevational gradients will accommodate the large majority of such upslope shifts. We urge that conserving intact tropical elevational gradients become a global goal, and suggest that synergies between biodiversity conservation and the ecosystem services provided by forested tropical mountains (e.g. watershed conservation) provide useful frameworks for translating this scientific recommendation into political reality.

**ACKNOWLEDGMENTS.** We thank numerous local landowners for facilitating our research, particularly J. Anuabo, L. Gande, S. Banu, J. Buga Tane, W. Paro and D. Goma from Karimui. J. Diamond assisted in planning resurveys, and comments from J. Diamond, K. Feeley, J.

Fitzpatrick, S. Freeman, W. Hochachka and M. Tingley, the handling editor and one anonymous reviewer greatly improved this manuscript. F. La Sorte assisted in extracting climate data from the CRU database, and G. Becker helped prepare Figure 1. Fieldwork was supported by grants from the Athena Fund of the Cornell Lab of Ornithology, the Explorer's Club, and by NSF GRFP 2011083591 to BGF. We dedicate this paper to N. Martin, Dr. T. Ihle, Dame C. Kidu, Sir P. Barter, P. Toko, P. Navratil, and B. and V. Middleton.

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CHAPTER 2

# THERMAL TOLERANCES TO COLD DO NOT PREDICT UPPER ELEVATIONAL LIMITS IN NEW GUINEAN MONTANE BIRDS

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**ABSTRACT**

I tested the predictions of the "fundamental physiological niche" hypothesis that thermal tolerances are tightly correlated with upper elevational limits in New Guinean montane birds. I combined previously published data describing New Guinean montane birds' 1) metabolic responses to temperature, 2) elevational distributions, and 3) recent upslope shifts, with an empirically measured lapse rate (temperature-elevation regression) to test two predictions of the fundamental physiological niche hypothesis—that species' thermal tolerances to cold temperatures, measured as lower critical temperatures and thermal conductances, are correlated with their upper elevational limits ($n$ = 24 species), and that species' thermal mismatches (the difference between the mean temperatures species experience at their upper elevation limits and their lower critical temperatures) predict the magnitude of recent warming-associated upslope shifts ($n$ = 11 species). Species' lower critical temperatures and thermal conductances were not

correlated with the ambient temperatures they experience at their upper elevational limits (cold range limit), and species' thermal mismatches were not related to the magnitude of recent upslope shifts at their upper elevational limits. My results do not support the fundamental physiological niche hypothesis and suggest New Guinean montane birds' upper elevational limits are unlikely to be set by the direct influence of temperature on adult birds' thermal tolerances. I also found no evidence that warming-associated upslope shifts in this avifauna are related to species' thermal physiology. While this result is based on a small sample size, it is consistent with the hypothesis that recent upslope shifts result from biotic factors indirectly related to temperature.

## INTRODUCTION

Tropical mountains harbor some of the most biodiverse floras and faunas on Earth (Myers et al., 2000). Temperature declines predictably with increasing elevation along tropical elevational gradients that span from hot lowlands to cold high-elevation forests and grasslands above treeline (Janzen, 1967). Because most tropical montane species inhabit narrow elevational distributions (Patterson et al., 1998; McCain, 2009) and seasonal temperature variation in the tropics is minimal, tropical montane species typically experience a relatively narrow range of environmental temperatures, particularly within closed canopy forest (Janzen, 1967). Thus, elevational specialization in tropical montane species may be associated with physiological adaptation to the thermal conditions found within a particular elevational zone (Ghalambor et al., 2006; Deutsch et al., 2008; Bozinovic et al., 2011). Supporting the hypothesis that temperature is a strong influence on the elevational limits of tropical montane species, tropical plants (Feeley et al., 2011; Jump et al., 2012), ectotherms (Raxworthy et al., 2008; Chen et al., 2009) and

endotherms (Forero-Medina et al., 2011; Freeman & Class Freeman, 2014) are shifting upslope at rates significantly associated with local temperature increases due to global warming.

However, the mechanisms by which temperature influences tropical montane species' elevational limits remain unclear. One possibility is that temperature directly influences species' elevational limits, a hypothesis termed the "fundamental physiological niche" hypothesis by Jankowski et al. (2012). This scenario hypothesizes that montane species' physiological adaptations to specific thermal environments limit their elevational distribution (Janzen, 1967; Deutsch et al., 2008; Kellermann et al., 2012). The fundamental physiological niche hypothesis predicts that thermal physiology largely sets species' elevational limits; thus, this hypothesis predicts species' thermal tolerances are tightly linked with the ambient temperatures a species experiences at its elevational margins (Jankowski et al., 2012). In this view, recent warming-associated upslope shifts result from species tracking their preferred thermal environments as temperatures increase (Colwell et al., 2008; Deutsch et al., 2008; Sinervo et al., 2010). While the fundamental physiological niche hypothesis may especially apply to tropical ectothermic species (Buckley et al., 2008; Deutsch et al., 2008; Tewksbury et al., 2008), tropical endotherms' distributions may also be directly affected by the temperatures they experience (McCain, 2009; Krockenberger et al., 2012; Khaliq et al., 2014). An alternate perspective is that temperature influences species' elevational limits through indirect effects. For example, species' range margins (and their warming-associated upslope shifts) could be controlled primarily by biotic interactions that may themselves ultimately link to temperature (Davis et al., 1998; Tylianakis et al., 2008; Thomas, 2010), or by interactions between direct and indirect influences of temperature (e.g., Helland *et al.* 2011).

It is important to recognize that, in reality, there is not a dichotomy between whether temperature directly or indirectly influences distributions, but rather a gradient between the relative effects of abiotic and biotic pressures, and their interaction, on species' distributional limits. Nevertheless, situations where temperature is a strong direct influence on distributional limits make qualitatively different predictions regarding the relationship between species' thermal tolerances and their environmental distributions than situations where temperature exerts a weak direct influence on distributional limits. Thus, it is useful to consider the predictions of the fundamental physiological niche hypothesis

The thermoneutral zone is the range of ambient temperatures over which a species is able to maintain its basal metabolic rate (Hill et al., 2012). The thermoneutral zone thus describes a "comfort zone" for endotherms, which must respond to ambient temperatures outside their thermoneutral zone (below and above their lower and upper critical temperatures, respectively) by increasing their metabolic rate and incurring an energetic cost (Hill et al., 2012). Given that species vary in their lower critical temperatures (LCTs) (Araújo et al., 2013; Khaliq et al., 2014), a clear prediction is that species inhabiting colder environments should have lower LCTs than related species inhabiting warmer environments (Kellermann et al., 2009; Sunday et al., 2012; Khaliq et al., 2014). In addition, the rate at which species increase their metabolic rate when exposed to temperatures below their LCT—their thermal conductance— may also reflect physiological adaptation to environmental conditions. Specifically, species in colder environments may be able to increase their metabolic rate when exposed to sub-LCT temperatures at a lower rate than species from warmer environments (McNab, 2002). Finally, the degree to which species' LCTs match their environments can be quantified as their thermal mismatch, with negative values for species that live in environments where temperatures are

colder than their LCT. If thermal tolerances are an important factor directly setting montane species' distributions, most species should have relatively small positive thermal mismatches, and the degree of thermal mismatch can serve as a proxy for sensitivity to temperature (e.g., when examining warming-associated upslope shifts).

I investigated the relationship between species' thermal tolerances to cold and their upper elevational limits by studying New Guinean montane birds that are shifting upslope at both warm and cold range limits (Freeman & Class Freeman, 2014). I combined documented warming-associated shifts with a dataset of species' metabolic responses to temperature (McNab, 2013) and an empirically-derived temperature elevation regression (lapse rate) to assess two predictions of the fundamental physiological niche hypothesis; 1) montane species that experience lower mean ambient temperatures at their upper elevational limit (cold range limit) should have lower LCTs and lower thermal conductances, and 2) montane species with smaller thermal mismatches at their lower critical temperatures should undergo larger warming-associated upslope shifts than species with larger thermal mismatches.

## METHODS

### *Thermal physiology*

McNab (2013) measured metabolic responses to temperature in wild New Guinean montane birds at two sites in the Central Ranges of Papua New Guinea— Ambua Lodge (2,100 m; Southern Highlands Province) and Kumul Lodge (2,860 m; Enga Province). Briefly, McNab captured wild adult birds using mist nets in the late afternoon and measured rates of oxygen consumption of resting birds over a range of temperatures at night (detailed methods in McNab 2013) to calculate species' lower critical temperatures and minimal thermal conductances

(hereafter "thermal conductance"). When McNab (2013) reported multiple values of thermal conductances for a species, I used averaged values of thermal conductance for analysis.

Measured thermoneutral zones did not appear to vary for seven species that were measured at both sites (McNab 2013), although the higher elevation site had markedly colder temperatures (estimated mean ambient temperatures 10.9°C vs. 14.8°C, see below for details on the elevation-temperature relationship). This suggests intraspecific variation in thermal tolerances within New Guinea's Central Ranges may be small for adult montane birds, though additional data would be necessary to rigorously test this possibility. If populations exhibit local adaptation to different thermal environments, species with large elevational distributions (e.g., elevational breadths > 2,000 m) may exhibit differences in their thermal tolerances at the extremes of their elevational distributions. To minimize this possible effect, I limited my analysis to species that occupied largely montane distributions (mostly found above 1,000 m), using data for 24 species from 17 families (5.5 ± 3.4 individuals measured per species) for which McNab (2013) reported LCTs and thermal conductances. Because most species in this dataset have relatively narrow elevational distributions (mean elevational breadth ~1,400 m within the New Guinean Central Range), my analysis may be robust to intraspecific variation along the elevational gradient. I did not include in my analysis an additional nine montane species whose LCTs were measured to be below ~12°C but were not quantified more precisely (McNab 2013; see Discussion for further consideration of this issue). Finally, McNab (2013) measured upper critical temperatures (UCTs, which are relevant for species' warm range margins/lower elevational limits) for only a small number of the species he studied; thus, I restrict my analysis to species' LCTs and upper elevation limits.

*Elevational distributions, upslope shifts and the temperature-elevation relationship*

I used a single authoritative source (Pratt & Beehler, 2014) to define lower and upper elevational limits for each bird species. Tropical montane species may inhabit different elevational zones in different geographic regions (e.g., Terborgh & Weske, 1975; Diamond, 1986). Therefore, when species exhibited regional variation in the elevational distributions they occupied, I used species' elevational limits reported for the Central Range of New Guinea, the same biogeographic region where physiological measurements and warming-associated upslope shifts were taken. Regional scale field guide data typically includes extreme records and thus tend to overestimate species' elevational distributions. To address this issue, I used species' "typical" elevational distributions presented by Pratt and Beehler (2014), which represent the elevational zones where species are mostly found. Another potential difficulty in assigning elevational distributions is elevational migration. Several species of New Guinean frugivores (e.g., fruit-doves) and nectarivores (e.g., lorikeets) roam widely in search of food and are known to exhibit predictable elevational migrations (Pratt & Beehler 2014). However, this is unlikely to bias my analysis, as nearly all species in my dataset are insectivores that are not known to undertake elevational migrations. Finally, I used data from a recent resurvey of bird species' elevational limits along a single elevational gradient on Mt. Karimui, also located in the Central Ranges, to quantify species' warming-associated upslope shifts at cold range limits (Freeman & Class Freeman, 2014).

Temperature is relatively invariant at a single site over the annual cycle in the tropics, but declines predictably with increasing elevation (Janzen, 1967). Thus, a montane species' lower elevation limit is its warm range limit, and upper elevation limit its cold range limit. The negative relationship between elevation and temperature is quantified as the lapse rate, which typically ranges in tropical mountains between 0.5°C and 0.6°C decline per 100 m increase in

elevation (Terborgh & Weske, 1975; Chen et al., 2009; Forero-Medina et al., 2011). For this study, I used a lapse rate of 0.51°C per 100 m to relate bird species' elevational limits to mean temperatures. I empirically measured this lapse rate using data from iButton temperature loggers placed at eight locations (at elevational intervals of approximately 150 m) between 1,250 m and 2,175 m along an elevational gradient on Mt. Karimui, Chimbu Province, during field work in June-July 2012 (Freeman & Class Freeman, 2014). Temperature loggers were placed in closed canopy forest, both on the forest floor and 2 m above the ground. Height above ground did not appear to influence estimation of mean daily temperatures, which dropped from 19.5°C at 1,250 m to 14.7°C at 2,175 m.

Patterns of diurnal temperature variation (e.g., maximum and minimum temperatures) across elevation in the iButton data were similar to the pattern described above for mean temperature; I therefore used mean temperature to characterize thermal environments across the elevational gradient in New Guinea, while recognizing that local temperatures may vary substantially due to differences in microclimate such as exposure to direct sun and wind. While my iButton data described temperatures in Mt. Karimui closed canopy forest for a relatively short time period (~ 40 days), daily variation in temperature at single sites during this time was minimal during this time, with the temperature profile for 1,250 m (extremes: 17°C – 22.75°C) barely overlapping that of 2,175 m (extremes: 12.25°C – 18°C). Mt. Karimui is located roughly 150 km from the sites (Ambua and Kumul Lodges) where McNab's (2013) physiological measurements were taken. The temperature-elevation relationship measured on Mt. Karimui was statistically robust (mean temperature regression on elevation, $r^2 = 0.95$) and similar to lapse rates measured on other tropical mountains. Therefore, I applied the Mt. Karimui lapse rate to

estimate the mean ambient temperatures montane species experience at their elevational limits in New Guinea's Central Ranges.

*Data Analysis*

I used linear regression models to test the predictions that species' LCTs and thermal conductances predict the ambient temperatures at montane species' upper elevational limits ($n$ = 24 species). Species' traits may be influenced by their shared evolutionary history, complicating comparative analyses of trait evolution (Felsenstein, 1985). To test whether shared evolutionary history influenced trait evolution in my dataset, I used a posterior set of pruned trees from Jetz et al. (2012), in combination with phylogenetic generalized least-squares (PGLS; Martins & Hansen, 1997), to run phylogenetically-controlled regressions using the packages nlme (Pinheiro et al., 2013) and ape (Paradis et al., 2004) in the R programming environment (R Development Core Team, 2014). Internal branch lengths were scaled to Pagel's $\lambda$ model, which estimates the amount of phylogenetic signal present in the evolutionary history of a given character (Pagel, 1999; Blomberg et al., 2003). The $\lambda$ parameter varies from 0 (no phylogenetic signal) to 1 (phylogenetic signal equal to Brownian motion) in this model and therefore indicates the evolutionary lability of the trait in question. Pagel's $\lambda$ was estimated to be negative for both the LCT and thermal conductance PGLS models (-0.11 and -0.19, respectively), indicating that thermal trait values were slightly negatively correlated with evolutionary relatedness in my dataset. Thus, I report results from regression models instead of PGLS models.

The dataset I used contains three species represented by a single individual in McNab's (2013) data. To test whether results were driven by the inclusion of these three species, I also ran analyses omitting these three species. Again, Pagel's $\lambda$ was estimated to be negative for both the

LCT and thermal conductance PGLS models in the reduced dataset (-0.13 and -0.15, respectively). I therefore report values from regression models for the reduced dataset as well.

Last, I tested whether warming-associated upslope shifts at upper elevation limits (cold range limits) in New Guinean montane birds are larger in species with relatively small thermal mismatches at their lower critical temperature ($n$ = 11 species). I calculated species' thermal mismatches at their cold range limit as the difference between a species' LCT (°C) and the ambient temperature it experiences at its upper elevational limit. I then used linear regression models to test whether, at cold range limits, species with smaller (or negative) thermal mismatches—those species most likely to be limited by cold temperatures—have undertaken larger upslope shifts than species with larger, positive thermal mismatches.

**RESULTS**

Montane species' LCTs did not predict the mean temperatures estimated to occur at their cold range limit ($t_{22}$ = 0.45, $p$ = 0.66, adj. $r^2$ = -0.035, see Fig. 1).

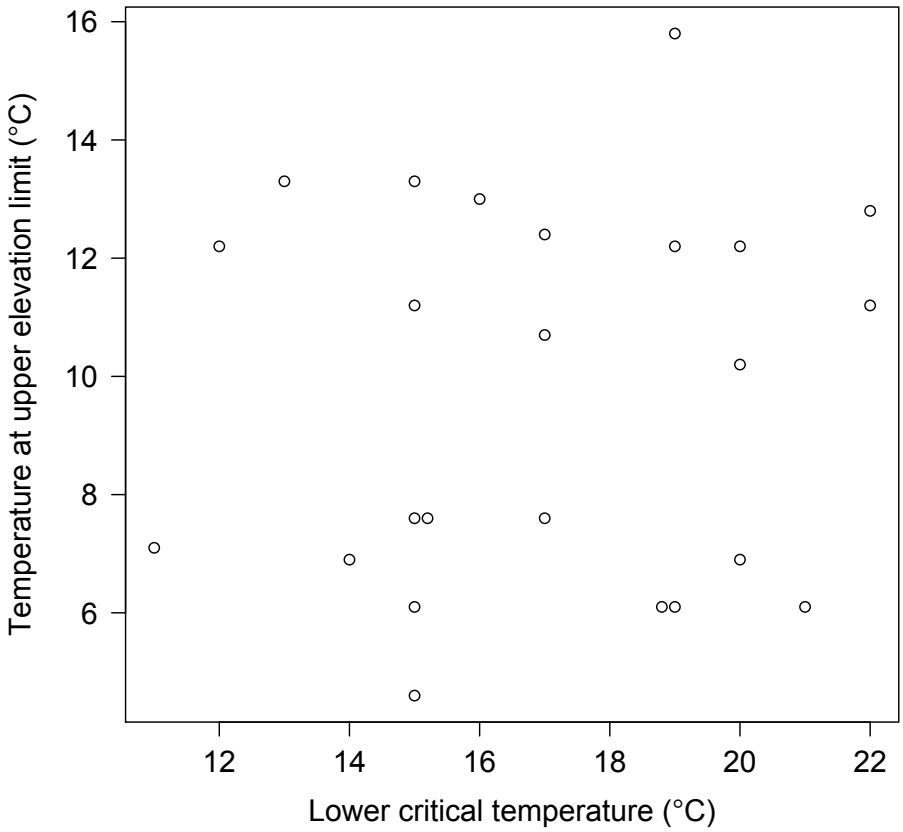


**Figure 1**. The relationship between species' lower critical temperatures and the mean temperatures they experience at their cold range limit (upper elevational limit) in New Guinean montane birds. Species' lower critical temperatures are unrelated to mean ambient temperatures at their upper elevational limit ($p = 0.66$).

Similarly, species thermal conductance values did not predict the mean temperatures estimated to occur at their cold range limit ($t_{22} =$ -0.19, $p = 0.85$, adj. $r^2 = -0.044$, Fig 2). I found similar results when using the reduced dataset, indicating that this lack of pattern was not driven by including species where thermal traits were measured for a single individual (reduced dataset—for LCT; $t_{19} = 0.47$, $p = 0.64$, adj. $r^2 = -0.041$, for thermal conductance; $t_{19} = 0.09$, $p = 0.93$, adj. $r^2 = -0.052$). These results echo previous studies indicating that basal metabolic rate is unrelated to elevation within tropical montane birds (McNab, 2013; Londoño et al., 2014).

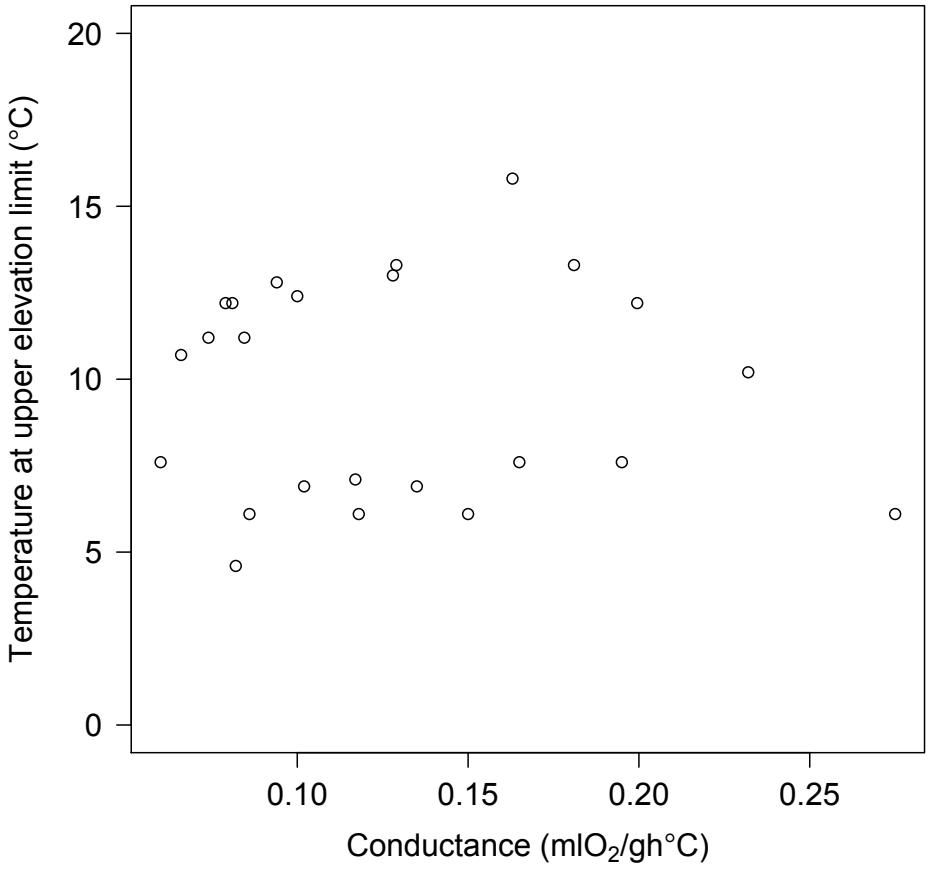


**Figure 2**. The relationship between species' minimal thermal conductances and the mean temperatures they experience at their cold range limit (upper elevational limit) in New Guinean montane birds. Species' minimal thermal conductances are unrelated to mean ambient temperatures at their upper elevational limit ($p = 0.85$).

The majority of tested species (88%) experience a thermal mismatch at their cold range margin (thermal safety margins at cold limit = -7.0 ± 4.6°C, Fig. 3; negative thermal safety margins indicate thermal mismatches), with most species experiencing a thermal mismatch (mean ambient temperatures colder than their LCT) at the site where they were captured and measured.

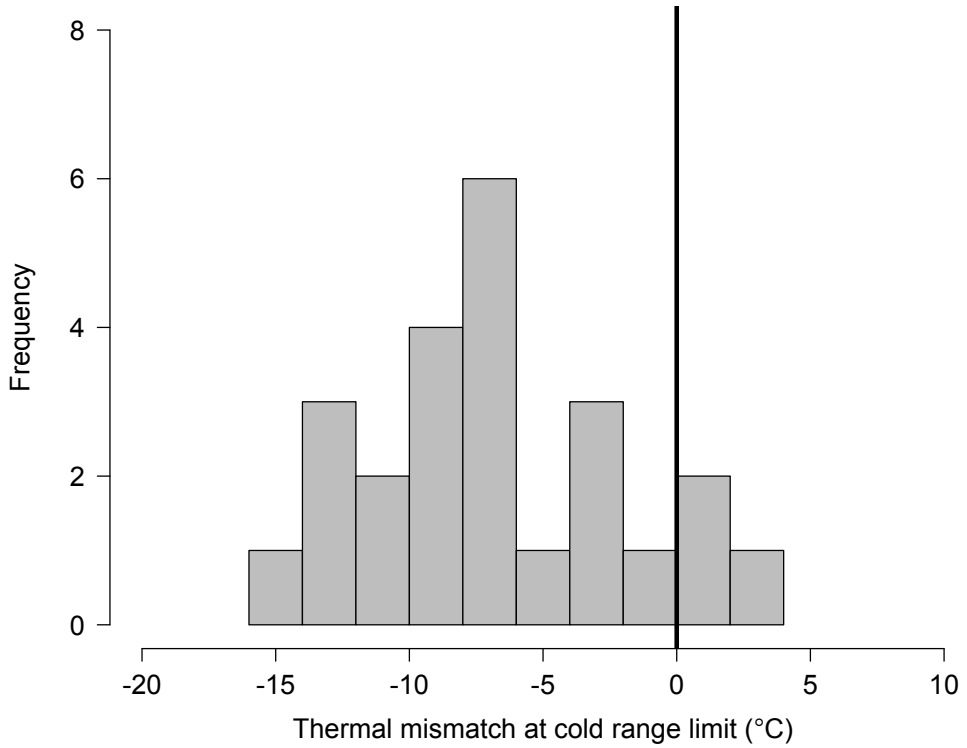


**Figure 3.** Thermal mismatches of New Guinean montane bird species at their cold range limits. Most species have large thermal mismatches at their cold range limits, indicating that most species live at elevations where mean ambient temperatures are colder than their lower critical temperature.

Thermal microclimates and behavior may minimize the degree to which birds at high elevations actually experience temperatures below their LCT. Taken at face value, however, these data suggest that montane New Guinean birds regularly occur at elevations up to 1,000 m higher than predicted if their upper elevational limits were strictly set by their lower critical temperature. If temperature directly influences warming-associated upslope shifts via impacts mediated by thermal physiology, then species with large negative thermal mismatches (i.e. species that are experiencing the most suboptimal thermal environments) are predicted to exhibit stronger upslope shifts than species with small negative or positive thermal mismatches. However, species' thermal mismatches were not related to the magnitude of their upslope shift

on Mt. Karimui at their cold range limit ($t_9 = 1.48$, $p = 0.17$; Fig. 4), though this analysis is based on a small sample size and should be viewed as preliminary.

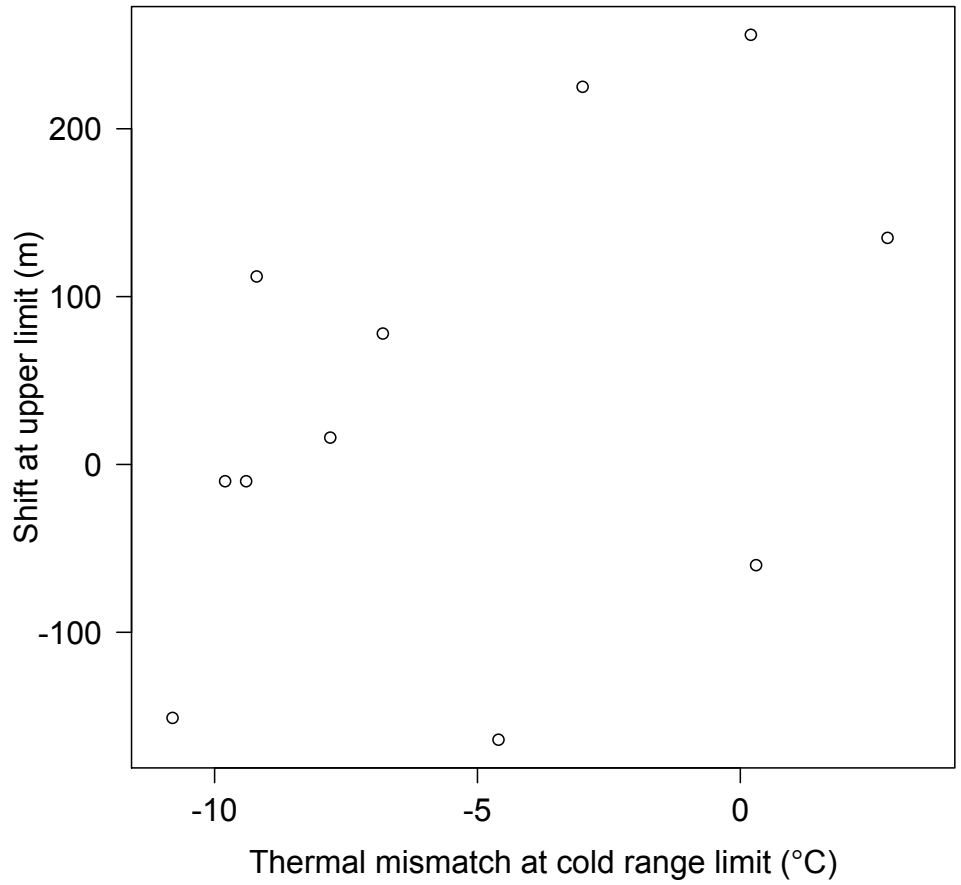


**Figure 4.** The relationship between New Guinean montane birds' thermal mismatches and their recent upslope shifts at cold range limits on Mt. Karimui. Species' thermal mismatches were unrelated to their upslope shifts at cold range limits ($p = 0.17$).

## DISCUSSION

New Guinean montane birds have shifted their distributions upslope by around 100 m at both warm (low elevation) and cold (upper elevation) range limits in the past half century (Freeman & Class Freeman, 2014). These shifts are significantly associated with recent local temperature increases (Freeman & Class Freeman, 2014), indicating that temperature is an important factor that directly or indirectly influences elevational limits in this avifauna. The fundamental

physiological niche hypothesis predicts that montane species' elevational distributions are tightly linked to their thermal tolerances. However, I found that species' LCTs and thermal conductances were not correlated with the mean ambient temperatures species experience at their upper elevational limits. In addition, species' thermal mismatches were unrelated the magnitude of their upslope shifts at their cold range limit (albeit with a small sample size). These results do not support the fundamental physiological niche hypothesis in New Guinean montane birds (applied to their upper elevation limits) and suggest that species' thermal tolerances do not greatly influence species' upper elevational limits in this avifauna.

These results could be influenced by the coarse way I characterized species' thermal environments. For example, the mean temperatures I estimated to occur at species' upper elevational limits might not represent the actual temperatures birds experience due to microclimatic variation, exposure, vegetation structure and other factors. However, most species in this dataset are found in the understorey or midstorey of closed canopy forest, where temperature fluctuations are minimal compared with more exposed microhabitats, suggesting that the mean temperatures I used to characterize thermal environments are appropriate for this analysis.

These results also depend on the underlying data used for analysis. For example, the conclusion that species' thermal mismatches at their cold range limit were unrelated to the magnitude of upslope shifts is based on a small sample of species ($n$ = 11), and should therefore be considered a preliminary result (though the apparent trend within this small sample is opposite that predicted by the fundamental niche hypothesis). In addition, while results were robust to the inclusion of species for which thermal trait data was measured in a single individual, adding further species to the dataset could potentially alter conclusions. For example, McNab (2013) did

not calculate LCT values for nine montane species with low (< 12°C) LCTs, and these species could therefore not be included in my analyses. If these omitted species with especially low (but unmeasured) LCTs tended to have particularly high upper elevational limits, the resulting analysis could be biased against finding a relationship between LCTs and upper elevation limits. However, there were three examples where omitted species had congeners present in the dataset that both occupied higher elevation (colder) environments and had higher ( > 12°C) LCTs. Thus, in these three cases, the congener present at higher (colder) elevations had a higher LCT, contrary to the predictions of the fundamental physiological niche hypothesis and suggesting that the omitted species are unlikely to bias the conclusions of this study. Finally, this study concerns variation in thermal tolerances within montane species of New Guinean birds only, and cannot address other important questions, such as whether species' elevational limits are influenced by their thermal performance curves, whether montane and lowland species consistently differ in their thermal physiology, or the degree to which thermal traits are plastic and reflect acclimation to the thermal environments experienced by adult birds.

Understanding how species' thermal tolerances are linked to their distributional limits at warm and cold range margins is an important goal of climate change ecology. In endotherms, a global analysis found little variation in heat tolerance in interspecific comparisons inhabiting different thermal environments but wide variation in cold tolerance, suggesting greater potential for evolutionary responsiveness to cold than heat across taxa (Araújo et al., 2013). Species in my analysis also showed variation in their tolerance to cold, with species' LCTs measured by McNab (2013) at the same site in the New Guinean Central Range ranging from 11°C to 22°C. However, I found that this variation in species' cold tolerances was not linked to the ambient temperatures they experience. This result is broadly consistent with global analyses that show the

correlation between species' thermal limits and the ambient temperatures they experience tends to be weak in endotherms (birds and mammals; Araújo et al., 2013; the same relationship is strong in ectotherms; Sunday et al. 2012, Araújo et al., 2013, Sunday et al., 2014).

The prevalence of thermal mismatches in my dataset demonstrates that many New Guinean montane birds are likely paying an energetic cost to live at high elevations. This conclusion applies to adult birds— the thermal tolerances of developing eggs and nestlings of New Guinean montane birds are unknown. If thermoneutral zones of eggs and nestlings are assumed to be similar to or more restricted than those of adults (Webb, 1987), then this conclusion would extend to individuals regardless of life stage. Presumably, food resources are sufficiently plentiful within New Guinean montane forests (and possibly benign thermal microclimates sufficiently common) that montane bird species at high elevations can meet their elevated energy requirements. Recent warming in New Guinea has presumably lessened this energetic cost, at least for individuals within the historic elevational distribution occupied by a species. However, the large majority of species are moving upslope at a rate that roughly tracks local temperature increases (Freeman & Class Freeman, 2014), such that populations as whole are likely experiencing similar thermal pressures through time. While physiological adaptation to abiotic factors undoubtedly impacts distributions of tropical montane birds in some cases (e.g., DuBay and Witt 2014; see also adaptation to hypoxia at very high elevations; e.g., Cheviron and Brumfield 2009; McCracken *et al.* 2009), I did not find support for the fundamental physiological niche hypothesis as applied to cold range limits of New Guinean montane birds.

This result suggests that biotic factors may be important in setting elevational limits of New Guinean montane birds. Limiting biotic factors could include resource availability (Ferger et al., 2014), habitat structure (Diamond, 1972; Ferger et al., 2014) and the presence of

competitors (Terborgh & Weske, 1975; Diamond, 1986; Tingley et al., 2014), natural enemies (Ricklefs, 2010) and mutualists (Callaway et al., 2002; Afkhami et al., 2014). In order to explain why species are shifting upslope in concordance with recent local warming, these biotic factors would have to link to temperature. For example, temperature may have a strong effect on habitat structure (e.g., affecting the lower elevation limit of cloud forest habitat) which in turn influences bird species' elevational distributions (Diamond, 1972). Ectotherms' distributions tend to be tightly correlated with temperature (Sunday et al. 2012, Araújo et al., 2013, Sunday et al., 2014)—if warming directly impact distributions and abundances of ectotherms that are important food resources (Ferger et al., 2014), disease vectors (Van Riper III et al., 1986), or nest predators (Jankowski et al. 2012), birds' distributions may change as a result. Finally, the outcomes of species interactions that influence distributional limits may themselves vary depending on ambient temperatures (Davis et al., 1998; Tylianakis et al., 2008; Helland et al., 2011).

In conclusion, I show that species' thermal tolerances to cold in a group of tropical endotherms (New Guinean montane birds) are not correlated with their upper elevational limits and appear not to explain why some species are rapidly moving upslope at their cold range margin in association with recent local warming while others are not. These results do not support the fundamental physiological niche hypothesis, at least when using species' LCTs and thermal conductances to quantify species' thermal physiologies. Further studies should test whether similar patterns occur in other montane avifaunas, and in other taxonomic groups, ideally directly measuring energy expenditure across a range of biologically relevant temperatures. Finally, the apparently limited influence of temperature to setting elevational limits in New Guinean birds is consistent with the hypothesis that biotic factors indirectly linked to

temperature may regulate elevational limits in this avifauna. Tropical mountains are the most biodiverse terrestrial ecosystems on Earth (Myers et al., 2000), and preliminary evidence suggests tropical montane species are disproportionately sensitive to temperature increases (Colwell et al., 2008; McCain & Colwell, 2011; Freeman & Class Freeman, 2014). Thus, research investigating the biotic factors that limit elevational distributions in New Guinean montane birds and other tropical montane biotas is urgently needed to conserve tropical montane hyperdiversity in the face of global warming and other environmental change.

**ACKNOWLEDGMENTS**

Comments from A. Agrawal, A. Class Freeman, S. Freeman, J. W. Fitzpatrick, B. McNab and two anonymous reviewers greatly improved this manuscript. This material is based upon work supported by the National Science Foundation Graduate Research Fellowship under Grant No. 2011083591.

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CHAPTER 3

# LIMITED EVIDENCE FOR BERGMANN'S RULE BODY SIZE CLINES IN PASSERINES ALONG TROPICAL ELEVATIONAL GRADIENTS

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**ABSTRACT**

I tested whether intra and interspecific patterns in body mass along elevational gradients follow Bergmann's Rule for a subset of tropical montane passerines, using tropical elevational gradients in New Guinea (Huon Peninsula and Central Ranges), Malaysian Borneo, Manu National Park in southeastern Peru and the Caribbean slope of Costa Rica.

I assessed intraspecific patterns in body mass for 19 common New Guinean passerines found along two elevational gradients. I evaluated interspecific patterns in body mass using two datasets. First, I compiled a list of closely related species that inhabit different portions of elevational gradients in four regions (species-pairs; New Guinea: $n = 45$, Borneo: $n = 22$, Peru: $n = 58$ and Costa Rica: $n = 30$). I then tested whether i) the upper elevation species had larger masses, ii) upper elevation species had greater mass disparities, and iii) species pairs with more divergent environmental distributions (reduced elevational overlap) had greater mass disparities.

Second, I used a comparative phylogenetic approach to test whether species' midpoint elevations predicted their masses in the entire passerine avifaunas found along single elevational gradients in New Guinea ($n$ = 184), Peru ($n$ = 529) and Costa Rica ($n$ = 220). In New Guinean passerines, upper elevation individuals did not tend to have larger masses than lower elevation conspecifics. Upper elevation species within species-pairs did not tend to have larger masses, but did have greater mass disparities. However, mass disparity was not related to elevational overlap. When considering entire passerine avifaunas along single elevational gradients, species' masses were not correlated with their midpoint elevational distributions. I found limited evidence that tropical montane passerines tend to have larger body masses at higher elevations. This analysis suggests mean temperature is not a generally important driver of body size evolution in tropical montane passerines.

## INTRODUCTION

Body size is an ecologically influential trait that varies widely within and among species (LaBarbera 1989; Brown et al. 2004). While various abiotic and biotic mechanisms can drive the evolution of body size (Brown et al. 2004), temperature is one potentially important abiotic factor influencing body size evolution—Bergmann's Rule describes the pattern that populations or species of endotherms living in colder environments tend to be larger than related populations or species living in warmer environments (Bergmann, 1847; James, 1970). The proper formulation of Bergmann's Rule remains debated; perhaps most importantly, Bergmann's Rule has been considered both a pattern (a negative relationship between body size and temperature) and a process (temperature exerts selection on body size through physiological mechanisms such as thermoregulation; e.g., Watt et al., 2010; Meiri, 2011; Olalla-Tárraga, 2011; Watt & Salewski,

2011). Studies investigating Bergmann's Rule have traditionally analysed body size clines along latitudinal gradients (e.g., Ashton, 2002; Ashton & Feldman, 2003; Feldman & Meiri, 2014; Watt et al., 2010). Temperature declines not only with increasing latitude but also with increasing elevation; thus, studies have also analysed whether Bergmann's Rule patterns are found in body size clines along elevational gradients (e.g., Brehm & Fiedler, 2004; Herzog et al., 2013).

Tropical elevational gradients offer an excellent geographic arena to investigate whether body size clines are associated with temperature. Temperatures decline over short distances along tropical mountain slopes, where ambient mean temperature drops ~ 5-6° C per 1,000 m gain in elevation (Forero-Medina et al., 2011; Freeman & Class Freeman, 2014a). As a consequence, sites on steep slopes may be located just a few km apart but experience very different temperatures. Because temperature variation is typically minimal at particular sites along tropical elevational gradients (e.g., daily temperatures at a given site vary by ~ 5° C, and annual variation is typically minor), sedentary tropical organisms separated by even small (~ 750 m) expanses of elevation can experience completely distinct temperatures, at least in the shaded forest interior (Janzen, 1967).

Evidence that tropical and subtropical montane faunas exhibit body size clines consistent with Bergmann's Rule along elevational gradients is mixed. Increases in body size in colder environments have been found intraspecifically in an Asian frog (Lu et al., 2006) and a Hawaiian songbird (Vanderwerf, 2012), and in interspecific comparisons in clades of Neotropical frogs (Gouveia et al., 2013) and lizards (Cruz et al., 2005; Zamora-Camacho et al., 2014) but not in clades of Asian frogs (Hu et al., 2011) or Neotropical butterflies (Hawkins & Devries, 1996), moths (Brehm & Fiedler, 2004), or dung beetles (Herzog et al., 2013). Results can be

inconsistent within a taxonomic group in a single geographic region. For example, patterns of intraspecific body size variation in Andean birds follow Bergmann's Rule in some (Graves, 1991), but not all (Remsen Jr, 1984; Remsen, 1993) species, including an example where a species exhibits Bergmann's Rule body size clines across latitudinal but not elevational gradients (Gutiérrez-Pinto et al., 2014). This inconsistency holds for analyses at the interspecific level as well, where some clades of tropical birds exhibit Bergmann's Rule body size clines while others do not (Blackburn & Ruggiero, 2001), suggesting that multiple mechanisms drive the evolution of body size clines along tropical and subtropical elevational gradients.

Thus, it remains unclear whether tropical montane birds generally exhibit larger body masses at higher (colder) elevations, as predicted by Bergmann's Rule. I addressed this question by testing how body sizes in the largest group of tropical montane birds—the passerines—are related to their elevational distributions. I consider Bergmann's Rule to simply be a negative relationship between body size and temperature (i.e., a pattern; hereafter "Bergmann's Rule"). As such, Bergmann's Rule predicts that 1) within species, individuals should tend to be larger at high elevations, 2) within species-pairs of closely related species upper elevation species should be larger than lower elevation species, with this relationship strongest in species-pairs that inhabit non-overlapping elevational distributions (and thus experience different ambient temperatures), and 3) when accounting for phylogenetic relationships, elevational distributions should be significantly related to body size in large assemblages of species. I tested the first prediction using field data for 19 common species of New Guinean understorey passerines captured along two single elevational gradients, the second using species-pairs of closely related species that inhabit minimally overlapping elevational distributions along an elevational gradient in four distinct tropical montane regions (the Eastern highlands of New Guinea, Manu National

Park in the Peruvian Andes, the Caribbean slope of Costa Rica, and the highlands of Malaysian Borneo), and the third using phylogenetic comparative methods to assess whether species' midpoint elevational distributions significantly predicts their body size in the entire passerine avifaunas found in three regions (the Eastern highlands of New Guinea, Manu National Park in the Peruvian Andes, and the Caribbean slope of Costa Rica). Taken together, these analyses—covering intraspecific and interspecific comparisons at shallow (closely related species-pairs) and deep (entire passerine avifaunas) phylogenetic scales, and replicated in the evolutionarily distinct avifaunas of multiple biogeographic regions (e.g., Neotropics, Southeast Asia and Melanesia)—provide a test of whether tropical montane birds follow Bergmann's Rule.

## MATERIALS AND METHODS

### Intraspecific

Bergmann's Rule predicts that, within species, individuals should tend to have larger masses at high elevations. I tested this prediction using field body mass data gathered along two elevational gradients in Papua New Guinea: the YUS Conservation Area, Morobe Province, and the northwest ridge of Mt. Karimui, Chimbu Province. The YUS Conservation Area (hereafter YUS, approximate coordinates: -6.00, 146.84) is located on the northern scarp of the Saruwaged Range on the Huon Peninsula. Between 2010 and 2012, a team of fieldworkers conducted mist-net surveys in primary forest along a single elevational gradient from 230 m to 2,940 m in YUS; a total of 18 mist-net surveys were completed along 1-km trials cut along elevational contours at intervals of 120-200 m in elevation (see Freeman et al., 2013 for more information). On the northwest ridge of Mt. Karimui (approximate coordinates: -6.56, 144.76), a team of fieldworkers surveyed the understorey bird communities with mist nets along a continuous gradient of

primary forest between 1,150 m and 2,520 in June-July 2012 (see Freeman & Class Freeman 2014b for further details). At both sites, captured individuals were weighed using a 30-g Pesola spring scale for smaller species and a 100-g Pesola spring scale for larger species.

I compiled field body mass data for 19 common understorey passerines from seven families found within YUS (see Table 1). These species were commonly captured (mean number of weighed individuals = 101, range = 48-192 weighed individuals/species) across a range of elevations (mean elevational breadth of captured individuals = 1,092 m, range = 520-1,640 m). I additionally included field body mass data for two species that were included in the YUS data from Mt. Karimui ($n$ = 110 and 43 weighed individuals; elevational breadth = 850 m and 1,025 m, respectively). I then used linear regressions implemented in R (R Development Core Team, 2014) to test if, for each species, individuals captured at higher elevations tended to be heavier than individuals captured at lower elevations. I included sex as a predictor variable for three species in which males and females differ in plumage (Black Berrypecker (*Melanocharis nigra*), Fan-tailed Berrypecker (*Melanocharis versteri*) and Black Fantail (*Rhipidura atra*)), though note that juvenile males have female-like plumage in these species, and used a Bonferroni correction to account for the influence of multiple tests on statistical significance.

**Interspecific: Elevational replacements**

Bergmann's Rule predicts that, when closely related species inhabit different elevational zones, i) the upper elevation species should have a larger mass, and ii) this difference in mass should be positively correlated to elevational divergence within the species-pair (i.e., upper elevation species should have especially larger masses than their lower elevation relatives when species within a species-pair inhabit completely distinct elevational zones). I tested these predictions by

identifying species-pairs of closely related species (typically congeners) that occupied divergent elevational distributions (defined as species-pairs with elevational overlap < 50%; most species-pairs in this dataset had narrow elevational overlaps, with the median elevation overlap = 8.8% and the 75$^{th}$ percentile of elevational overlap = 23.2%). Such species-pairs are prominent in tropical montane faunas (Patterson et al., 1998; Pyrcz & Wojtusiak, 2002; Pasch et al., 2013) and are especially common in birds (Terborgh & Weske, 1975; Jankowski et al., 2010; Freeman & Class Freeman, 2014b). I used single references to compile species-pairs of passerine "elevational replacements" found along forested elevational gradients in four regions that feature large mountain ranges spanning from lowlands (< 400 m) to above treeline (> 3,500 m): the Eastern Highlands of New Guinea ($n$ = 45 species-pairs; Pratt & Beehler, 2014), Manu National Park in the Andes of southeastern Peru ($n$ = 58 species-pairs; Walker et al., 2006), the Caribbean slope of Costa Rica ($n$ = 30 species-pairs; Stiles et al., 1989) and Malaysian Borneo ($n$ = 22; Myers, 2009), and a single reference volume to quantify body masses for each species of elevational replacement (Dunning, 2007). I limited my analysis to forest passerines (hereafter "passerines"), as the majority of habitat in these regions is forest.

I used a sign test to assess whether cases where upper elevation species had larger masses than their lower elevation relatives ("high and heavy" species-pairs) outnumbered reversed cases ("low and large" species-pairs) in each region. This simple analysis does not consider quantitative differences in mass difference. I therefore calculated the mass disparity for each species-pair—the mass of the upper elevation species divided by the mass of the lower elevation species, such that positive mass disparities indicate "high and heavy" cases—and used t-tests to ask whether species-pairs within regions had significantly positive mass disparities. This analysis, in turn, overlooks differences in the degree to which species within species-pairs

experience different ambient temperatures. If colder temperatures are associated with larger body masses, as predicted by Bergmann's Rule, body mass disparities should be negatively correlated with elevational overlap (greater mass disparities in species-pairs that occupy distinct elevational zones that do not overlap). I tested this prediction using a t-test to examine whether species-pairs with non-overlapping elevational distributions ($n$ = 63, a subset of the total dataset) had mass disparities significantly greater than zero, and also a linear regression model, with mass disparity as the response variable and elevational overlap (scaled from 0 to 0.5) and region as predictor variables.

**Interspecific: Passerine avifaunas**

Finally, Bergmann's Rule predicts that elevational distributions should be significantly related to body mass in large assemblages of species when taking phylogenetic relationships into account. I tested this prediction using the passerine avifaunas found along elevational gradients in three distinct regions, the Eastern Highlands of New Guinea, Manu National Park in southeastern Peru, and the Caribbean slope of Costa Rica, using the same reference volume to quantify body masses for each species in each region (Dunning, 2007) and single sources (New Guinea: Pratt & Beehler, 2014; Costa Rica: Stiles et al., 1989; Peru: Walker et al., 2006) to define elevational ranges of all passerine species found in each region (New Guinea: $n$ = 184 species; Peru: $n$ = 529 species; Costa Rica: $n$ = 220 species). I did not include Malaysian Borneo in this analysis as body mass data was unavailable for many Bornean species. I characterized species' elevational distributions as their elevational midpoint.

I then used comparative phylogenetic methods to test whether species' elevational midpoints were significantly related to their mass while accounting for evolutionary relatedness

among species. I transformed both response and predictor variables using log transformations so that residuals conformed to a normal distribution. I used a phylogenetic tree from Jetz et al. ( 2012) that consisted of passerine taxa with genetic information ("Hackett sequenced species"), in combination with phylogenetic generalized least squares (PGLS, (Martins & Hansen, 1997), implemented using the packages nlme (Pinheiro et al., 2013) and ape (Paradis et al., 2004) in the R programming environment (R Development Core Team, 2014). I scaled internal branch lengths according to Pagel's λ model, which estimates the amount of phylogenetic signal present in the evolutionary history of a given character (Pagel, 1999; Blomberg et al., 2003). In this model, the λ parameter varies from 0 (no phylogenetic signal or a star phylogeny) to 1 (phylogenetic signal equal to Brownian motion or branch lengths remain unchanged) and therefore provides a convenient measure of evolutionary lability for the trait in question. I examined residual plots by eye and removed one outlier from the analysis of Costa Rican passerines. Results were very similar with and without this outlier; I present results of the model with the outlier excised. I also investigated using a Ornstein-Uhlenbeck (OU) model of trait evolution to investigate body mass evolution in each region, but OU models failed to converge and were thus unable to be parameterized (Ho & Ané, 2014). I therefore report only results of Pagel's λ models.

## RESULTS

### Intraspecific

Most species did not vary in body mass along the elevational gradients in YUS or Mt. Karimui (Table 1; no variation in body mass with elevation in 19 out of 21 comparisons).

**Table 1.** Results of mass/elevation regressions for New Guinean passerines. Sexually dimorphic species where sex was included as a covariate are marked with an asterisk. Elevational distribution describes the lowest and highest sites where a species was mist-netted and weighted along elevational gradients in the YUS Conservation Area and on Mt. Karimui. Statistical significance following Bonferroni correction ($P < 0.0024$) is indicated in bold.

| English name | Site | Mass (g) | *n* | Elevational distribution (m) | Coefficient | Standard Error | *P*-value |
|---|---|---|---|---|---|---|---|
| Long-billed Honeycreeper | YUS | 43.3 | 48 | 230 – 1790 | -0.0023 | 0.0016 | 0.16 |
| Rufous-backed Honeyeater | YUS | 21.4 | 178 | 1660 - 2550 | -0.0011 | 0.00091 | 0.27 |
| Rusty Mouse-Warbler | YUS | 15.2 | 53 | 390 - 1660 | 0.000028 | 0.00055 | 0.96 |
| Mountain Mouse-Warbler | YUS | 16.7 | 68 | 1790 - 2550 | -0.00071 | 0.00059 | 0.23 |
| Large Scrubwren | YUS | 14.1 | 130 | 1660 - 2550 | -0.00046 | 0.00036 | 0.21 |
| Black Berrypecker* | YUS | 13.1 | 96 | 230 - 1090 | 0.0013 | 0.00057 | 0.021 |
| Fan-tailed Berrypecker* | YUS | 13.8 | 136 | 1510 - 2550 | 0.0034 | 0.00074 | **0.000012** |
| Dwarf Longbill | YUS | 11.5 | 97 | 230 - 1790 | 0.00012 | 0.00038 | 0.76 |
| Slaty-chinned Longbill | YUS | 11 | 192 | 610 - 2420 | -0.000058 | 0.00037 | 0.88 |
| Slaty-chinned Longbill | Karimui | 11.4 | 110 | 1150 – 2000 | 0.00099 | 0.00050 | 0.051 |
| Little Shrike-Thrush | YUS | 34.5 | 125 | 230 - 1790 | -0.0026 | 0.00067 | **0.00014** |
| Rufous-naped | YUS | 37.4 | 49 | 1660 - 2550 | -0.00071 | 0.0015 | 0.63 |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| Whistler | | | | | | | |
| Regent Whistler | YUS | 21 | 67 | 1360 - 2550 | -0.0015 | 0.00066 | 0.025 |
| Black Fantail* | YUS | 11.3 | 143 | 910 - 2550 | -0.00039 | 0.00022 | 0.082 |
| Black Fantail* | Karimui | 11.9 | 43 | 1250 - 2275 | -0.0038 | 0.00052 | 0.48 |
| Spot-winged | YUS | | | 230 - 910 | | | |
| Monarch | | 16.8 | 93 | | -0.0011 | 0.00064 | 0.086 |
| Lesser Ground- | YUS | | | 1360 - 2280 | | | |
| Robin | | 31.4 | 60 | | -0.00029 | 0.0014 | 0.83 |
| Ashy Robin | YUS | 34.4 | 89 | 1660 - 2550 | -0.0028 | 0.0015 | 0.071 |
| White-eyed Robin | YUS | 33.5 | 116 | 750 - 1660 | -0.0015 | 0.00097 | 0.13 |
| White-rumped | YUS | | | 390 - 910 | | | |
| Robin | | 24.4 | 95 | | -0.00067 | 0.0018 | 0.71 |
| Slaty Robin | YUS | 24.4 | 81 | 1510 - 2420 | -0.00042 | 0.00078 | 0.59 |

After using a Bonferroni correction to account for multiple tests, two species in YUS showed a significant relationship between body mass and elevation. This relationship was positive in one case and negative in the other, providing equivocal support for intraspecific Bergmann's Rule body size clines in this dataset. First, the Little Shrike-Thrush (*Colluricincla megarhyncha*) has significantly smaller masses at higher elevations (Figure 1a)—a linear regression model predicts that Little Shrike-Thrushes in YUS are around 12% lighter at their upper elevation limit (1790 m) compared to their lower elevation limit (230 m). Second, Fan-tailed Berrypeckers (*Melanocharis versteri*) are significantly larger at higher elevations (Figure 1b). Specifically, female-plumaged Fan-tailed Berrypeckers are larger at higher elevations. Males are substantially smaller and do not vary in mass across their elevational range, suggesting this sex difference in mass along the YUS elevational gradient is not an artifact of juvenile males in dull female plumage being misclassified as females. It has been previously reported that

female *Melanocharis* species are larger than males (Pratt & Beehler, 2014), but I am unaware of previous reports that female-plumaged Fan-tailed Berrypeckers are larger at high elevations. The ecological significance of this pattern remains uncertain.

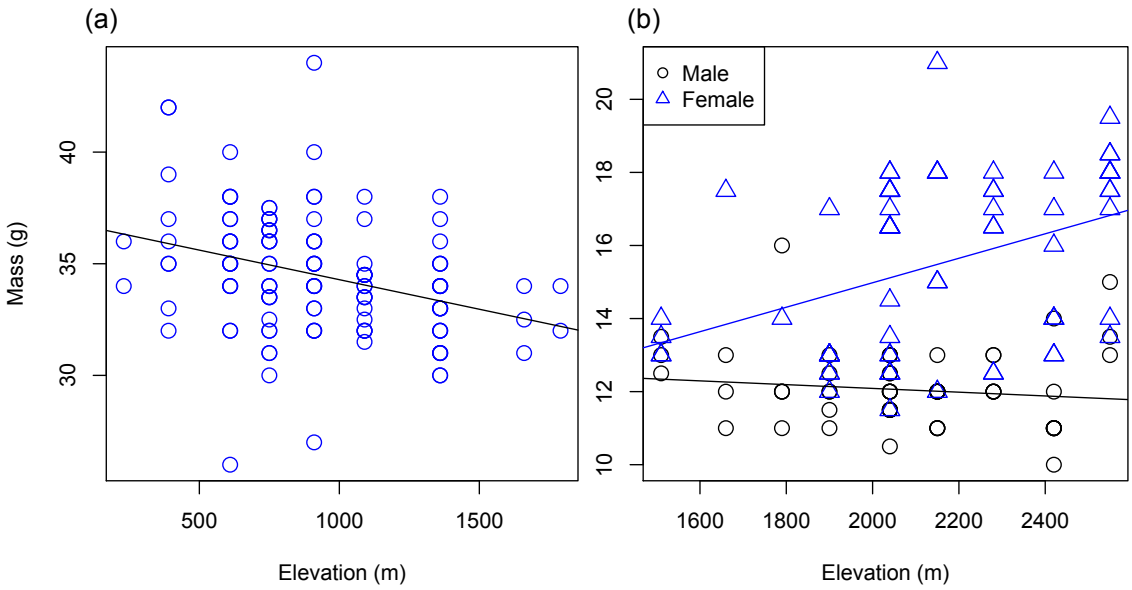


**Figure 1.** Two examples of intraspecific body size clines in New Guinean passerines along the YUS elevational gradient: a) Little Shrike-thrushes (*Colluricincla megarhyncha*) are smaller at high elevations and b) Fan-tailed Berrypecker (*Melanocharis versteri*) females (but not males) are larger at high elevations. Trendlines are from linear regression models. These examples are exceptions: most (19 out of 21 cases) New Guinean passerines did not show body size clines along elevational gradients.

**Interspecific**

In each region, "high and heavy" cases (where the upper elevation species had a larger mass) were not significantly more frequent than "low and large" cases (where the lower elevation species had a larger mass; *p*-values from sign tests = 0.20 to 1, Table 2).

**Table 2.** Regional patterns of body mass variation in elevational replacements of tropical montane passerines. Species-pairs were classified as "high and heavy" when the upper elevation species had a larger mass and "low and large" when the lower elevation species had a larger mass. P-values give results from sign tests within regions. Two species- pairs from Peru had identical body masses and body masses were unavailable for six species-pairs from Borneo.

| Region | "High and heavy" species-pairs | "Low and large" species-pairs | *P*-value |
|---|---|---|---|
| New Guinea (Eastern Highlands) | 23 | 22 | 1 |
| Peru (Manu National Park) | 28 | 28 | 1 |
| Costa Rica (Caribbean slope) | 19 | 11 | 0.20 |
| Borneo (Sabah) | 6 | 10 | 0.45 |

However, the difference in masses within a species-pair tended to be greater in "high and heavy" cases compared to "low and large" cases (Figure 2)—mass disparities were significantly positive in Peru (95% confidence interval for mass disparity = 0.0057 – 0.16; t = 2.16, df = 57, p = 0.035) and positive, though not significantly so, in each of the other three regions (New Guinea: 95% confidence interval for mass disparity = -0.037 – 0.17; df = 44, t = 1.28, p = 0.21; Costa Rica: 95% confidence interval for mass disparity = -0.015 – 0.17; df = 29, t = 1.70, p = 0.099; Borneo: 95% confidence interval for mass disparity = -0.075 – 0.27; df = 15, t = 1.21, p = 0.24).

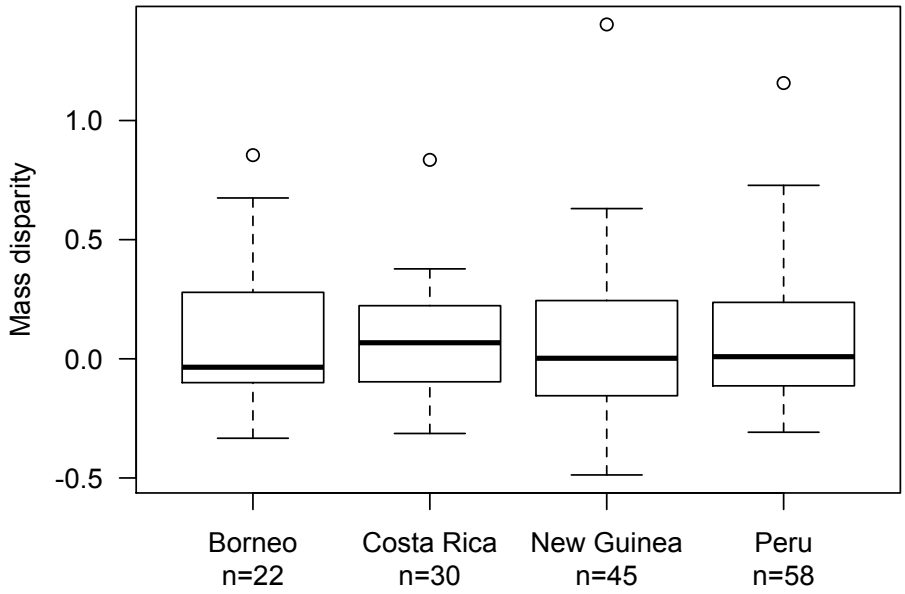


**Figure 2**. Mass disparity in species-pairs of elevational replacements in four regions. Boxplots illustrate median (horizontal black bar), first and third quartiles (boxes), and minimum and maximum values (points and dotted lines). While median values are close to zero, indicating similar numbers of cases with positive mass disparities (upper elevation species has larger mass) and negative mass disparities (lower elevation species has larger mass), mean mass disparity is positive in each region, and significantly so in Peru (denoted by an asterisk).

Last, mass disparities were not larger in species-pairs with less elevational overlap. When considering the subset of species-pairs with non-overlapping elevational distributions, mass disparities were not significantly different from zero ($n$ = 63 species-pairs; 95% confidence interval = -0.039 – 0.089, t = 0.79, df = 61, p = 0.43, see points at elevational overlap = 0 in Figure 3). In addition, parameter estimates for elevational overlap were not significantly different from zero in a linear regression model (Figure 3, Table 3).

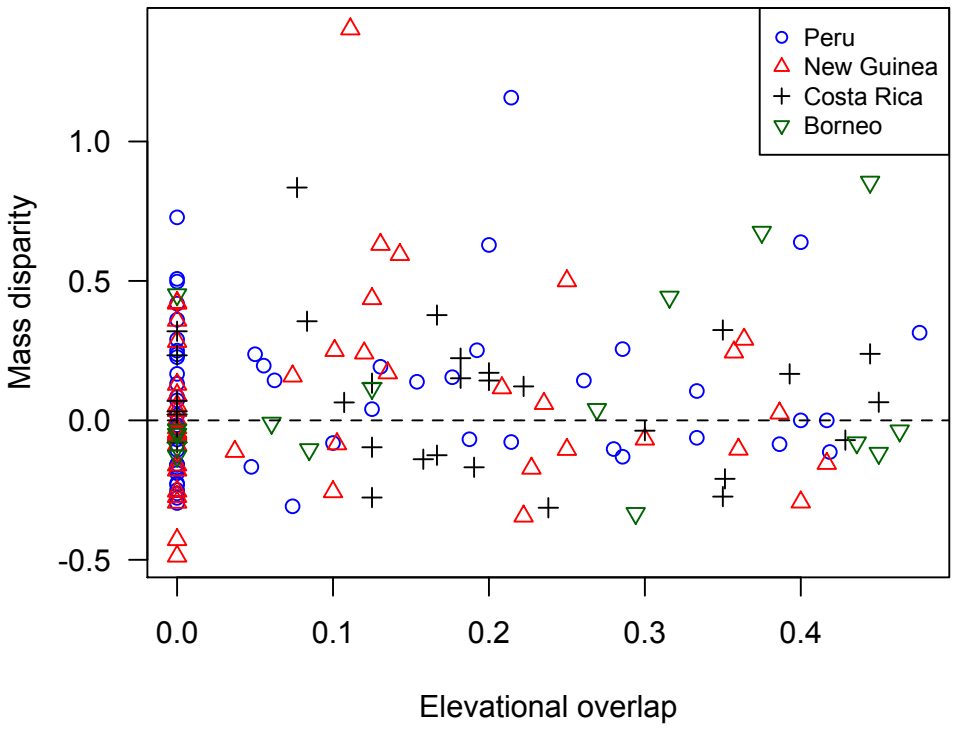


**Figure 3**. Elevational overlap is unrelated to mass disparity within species-pairs of elevational replacements in four regions. The dashed horizontal line at mass disparity = 0 serves to distinguish species-pairs with positive and negative mass disparities.

**Table 3.** Results of linear regression model predicting body mass disparity in species-pairs of elevational replacements.

| Parameter | Estimate | Std. error | *P*-value |
|---|---|---|---|
| Intercept | 0.0017 | 0.11 | 0.99 |
| Elevational overlap | 0.47 | 0.41 | 0.25 |
| Region: Costa Rica | 0.13 | 0.15 | 0.37 |
| Region: New Guinea | 0.051 | 0.13 | 0.69 |
| Region: Peru | 0.049 | 0.12 | 0.69 |
| Elevational overlap x Region: Costa Rica | -0.77 | 0.56 | 0.17 |
| Elevational overlap x Region: New Guinea | -0.37 | 0.52 | 0.48 |
| Elevational overlap x Region: New Guinea | -0.19 | 0.49 | 0.69 |

PGLS models for each region had lambda values very near 1, indicating relatively high phylogenetic signal in passerine body mass (Figure 4, Table 4). Parameter estimates for midpoint elevation in each model were not significantly different from zero, indicating that log midpoint elevation does not predict log body mass at the large phylogenetic scale of entire passerine avifaunas found along an elevational gradient.

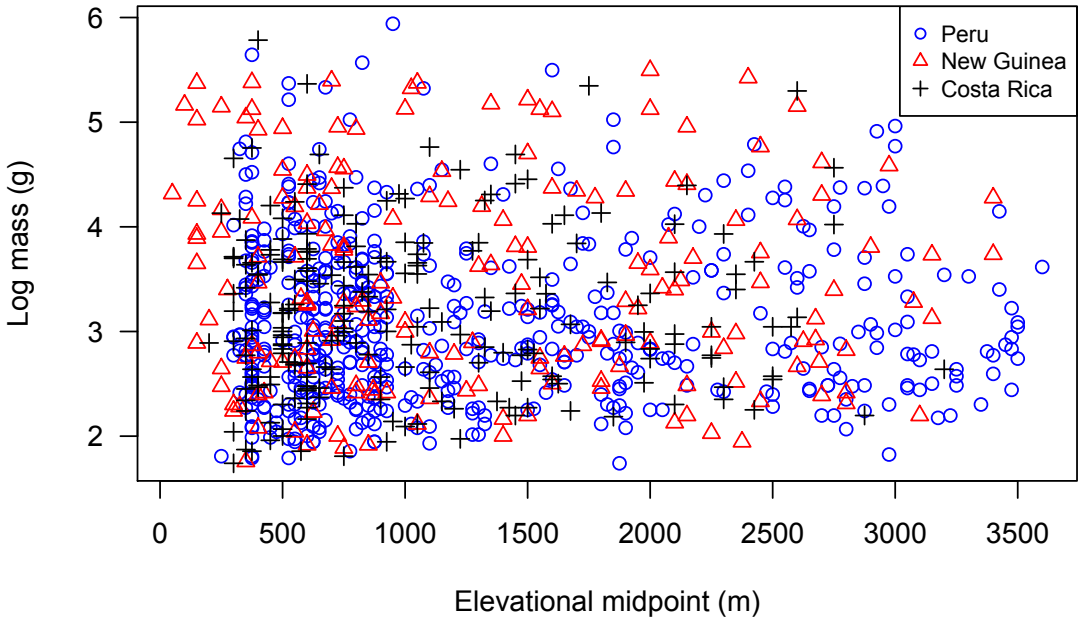


**Figure 4.** Elevational midpoint is unrelated to mass (log) in passerine avifaunas of three regions. Parameter estimates for elevational midpoint in phylogenetic generalized least squares models were not significantly different from zero.

**Table 4.** Results of Pagel's λ PGLS models examining the influence of log midpoint elevation on log body mass.

| PGLS model | λ | Parameter | Estimate | Std. Error | *P*-value |
|---|---|---|---|---|---|
| Peru (Manu National Park) | 0.99 | Log (midpoint elevation) | 0.018 | 0.030 | 0.56 |
| Costa Rica (Caribbean slope) | 1.0 | Log (midpoint elevation) | -0.086 | 0.053 | 0.11 |
| New Guinea (Eastern highlands) | 0.99 | Log (midpoint elevation) | 0.027 | 0.032 | 0.41 |

## DISCUSSION

Tropical montane passserines vary widely in body mass (Dunning, 2007). However, I found little evidence that this variation in body mass is related to species' elevational distributions. In tropical mountains, elevation is tightly correlated with temperature, making species' elevational distributions a convenient proxy for the environmental temperatures they experience. At the intraspecific level, a sample of New Guinean passerines typically did not vary in body mass along single elevational gradients (Table 1), with single case examples of significant decreases (Figure 1a) and increases (Figure 1b) in body mass with elevation. At the interspecific level, species' body masses were weakly related to their elevational distriutions at a shallow phylogenetic scale (when considering closely related species-pairs that inhabit different elevational zones; Tables 2 and 3, Figures 2 and 3) and unrelated to their body masses at deep phylogenetic scales (considering entire passerine avifaunas; Figure 4, Table 4). Given that the tropical montane passerines in this study did not demonstrate body size clines consistent with

Bergmann's Rule, the mechanistic processes of physiological adaptation hypothesized to underlie Bergmann's Rule seem unlikely to generally apply to tropical montane birds.

Previous published studies investigating body mass variation in birds have often found geographic patterns of body size clines consistent with Bergmann's Rule. For example, global analyses of intraspecific variation in avian body mass have found the strong pattern that populations in colder environments are typically larger than those found in warmer environments (Ashton, 2002; Meiri & Dayan, 2003). These studies included few tropical species and primarily considered body mass patterns along latitudinal gradients where differences in temperature covary with many additional abiotic (e.g., temperature seasonality) and biotic (e.g., species richness, resource seasonality) factors that may also influence body size evolution. Intraspecific patterns in tropical birds along elevational gradients are sometimes consistent with Bergmann's Rule (e.g., Vanderwerf 2012), but most New Guinean passerines (19 out of 21 comparisons) in this study did not vary in mass over an elevational gradient. The two exceptions were a significant decline in body mass with elevation in Little Shrike-Thrushes (Figure 1a) and an example of a significant increase in body mass with elevation in female, but not male, Fan-tailed Berrypeckers (Figure 1b). Further studies are necessary to test the possibility that intraspecific body size clines consistent with Bergmann's Rule are present in tropical montane passerines in species omitted in my analysis (e.g., canopy species that are poorly sampled with mist-nets), in other regions in New Guinea, or more generally in other tropical regions.

When comparing closely related species that inhabit different elevational distributions within each of four regions, I found equal proportions of cases where the upper elevation species had a larger mass ("high and heavy") and where the lower elevation species had a larger mass ("low and large"; Table 2). While the proportion of "high and heavy" and "low and large" cases

was similar, “high and heavy” examples tended to have greater difference in mass, and this relationship was significantly positive in one region (Peru). These results provide mixed support for a positive relationship between body size and elevation. However, the key prediction of the Bergmann’s Rule pattern, applied to species-pairs of elevational replacements, is that mass disparities are largest in species-pairs that inhabit non-overlapping elevational distributions. I found no evidence that this was the case in any region (Figure 3, Table 3), and also found no evidence that species elevational midpoints are related to their body mass in a comparative phylogenetic analysis of entire passerine avifaunas (Figure 4).

On the surface, my results contradict a previous study of Andean passerines that found correlations between species’ body masses and elevational midpoints (Blackburn & Ruggiero, 2001). One possible explanation for these different conclusions from studies of Andean passerines is spatial scale—instead of the entire avifauna found within a region (i.e., all Andean passerines), I used only the set of species found along a single elevational gradient in my analysis. However, in the regional analysis, midpoint elevation explained only 2% of variation in body mass, and many clades did not follow Bergmann’s Rule (Blackburn & Ruggiero, 2001). Thus, Blackburn and Ruggiero’s (2001) analysis also suggests that tropical montane passerines do not consistently show body size clines concordant with Bergmann’s Rule. This view accords with previous studies that found Bergmann’s Rule does not apply to other tropical montane faunas (Hawkins & Devries, 1996; Brehm & Fiedler, 2004; Herzog et al., 2013).

These results have implications for the relationship between elevational distribution and competitive dominance, as behavioral dominance in interspecific contests is typically associated with body size in birds (Robinson & Terborgh, 1995; Freshwater et al., 2014; but see Martin & Ghalambor, 2014). Recent field experiments have supported the long-standing hypothesis

(Terborgh & Weske, 1975) that asymmetric interspecific aggression can influence the elevational distributions of pairs of tropical elevational replacements (Jankowski et al., 2010; Pasch et al., 2013). Many tropical montane passerines are shifting their distributions upslope associated with recent warming (Forero-Medina et al., 2011; Freeman & Class Freeman, 2014a), and it has been hypothesized that asymmetric interspecific aggression between tropical elevational replacements may influence their rates of warming-associated upslope shifts (Jankowski et al., 2010). I found no consistent pattern in relative body mass between upper and lower elevation species-pairs of elevational replacements. Thus, if body mass is associated with behavioral dominance in tropical avian elevational replacements, relative elevational distribution is unlikely to predict interspecific aggression in these taxa. It is therefore likely that field studies will demonstrate both instances where larger lower elevation species are behaviorally dominant (and could conceivably "push" their upper elevation replacement upslope with continued warming; e.g., *Catharus* thrushes in Jankowski et al., 2010 and Freeman & Montgomery *in press*) and cases where larger upper elevation species are behaviorally dominant (and may be able to maintain their distributions in the face of continued warming as "kings of the mountain"; e.g., *Scotinomys* singing mice in Pasch et al., 2013).

In conclusion, I found little evidence that body masses of tropical montane passerines are related to the elevational zones they inhabit when considering the passerine species, species-pairs and entire avifaunas included in my analysis. I failed to find the pattern predicted by Bergmann's Rule at the intraspecific level for New Guinean birds and at the interspecific level in two analyses with large sample sizes conducted in multiple regions that contain largely evolutionarily independent passerine radiations. Because body size clines in tropical montane passerines do not conform to the pattern predicted by Bergmann's Rule, the hypothesized process of colder mean

temperatures selecting for larger body sizes is unlikely to generally apply to tropical montane passerines. Thus, mean temperature appears to exert a minimal (or idiosyncratic) influence on body size in tropical montane passerines. In this view, biotic factors (e.g., social selection, resource availability and species interactions) and the interplay between abiotic and biotic factors may be more important drivers of body mass evolution in tropical montane birds.

**ACKNOWLEDGEMENTS**

I thank two anonymous reviewers for comments that greatly improved this manuscript, T. Heaton and E. Sibbald for assistance compiling body mass data, and N. A. Mason for statistical advice. This material is based upon work supported by the National Science Foundation Graduate Research Fellowship under Grant No. 2011083591.

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CHAPTER 4

# COMPETITIVE INTERACTIONS UPON SECONDARY CONTACT DRIVE ELEVATIONAL DIVERGENCE IN TROPICAL BIRDS

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**ABSTRACT**

Tropical mountains harbor exceptionally high biodiversity in part due to the marked elevational stratification of tropical biotas. However, the factors that influence the evolution of elevational distributions remain uncertain. I used a database of sister species of tropical montane birds from 41 families and three regions— the Neotropics, Himalaya and New Guinea— to test whether patterns of elevational divergence were consistent with 1) a stochastic process, 2) ecological sorting of elevational divergence that occurred in allopatry, or 3) elevational divergence driven by competitive interactions upon secondary contact. The stochastic and ecological sorting hypotheses predict that increased elevational divergence in sympatric sister species is explained by their greater evolutionary age, while the competitive interactions hypothesis predicts that elevational divergence is explained by geographical overlap. I found that genetic distances were unrelated to elevational divergence, and that allopatric sister species occupied similar elevational distributions regardless of genetic distance in each region. Instead, sympatry was the only

significant predictor of elevational divergence—regardless of evolutionary age, sympatric sister species had greater elevational divergence than allopatric sister species in each region, as predicted by the competitive interactions hypothesis. Importantly, this pattern occurred in all three geographic regions, suggesting that competition-driven elevational divergence upon secondary contact is a general process of community assembly in tropical montane avifaunas.

## INTRODUCTION

Across taxa, biodiversity is concentrated in tropical latitudes (Mittelbach et al. 2007), with tropical mountains supporting disproportionately diverse biotas (Myers et al. 2000; Rahbek and Graves 2001; Jetz et al. 2004; Fjeldså et al. 2012). This montane 'megadiversity' occurs at two well-characterized levels. First, species richness is high at any given location (alpha diversity), especially in lower elevation forests (Patterson et al. 1998). Second, most species are only found within narrow elevational zones, leading to high species turnover (beta diversity) along elevational gradients (Patterson et al. 1998; Cadena et al. 2012). At an extreme, this turnover may involve closely related species that inhabit parapatric distributions along elevational gradients ('elevational replacements'; Diamond 1973; Terborgh and Weske 1975; Patterson et al. 1998; Freeman and Class Freeman 2014a).

That elevational specialization is rampant in tropical mountains is remarkable, because divergence in closely related species' climatic niche conditions is often minimal (Wiens et al. 2010; Cadena et al. 2012). This pattern – phylogenetic niche conservatism – can apply to climatic niches over both long (> 5 million years; Peterson et al. 1999; Peterson 2011) and short (decades; Chen et al. 2011; Petitpierre et al. 2012) time scales, and has been observed in phylogenetic analyses of extant taxa (e.g., Peterson et al. 1999; Peterson 2011), responses to

recent climate change along elevational gradients (e.g., Chen et al. 2011; Freeman and Class Freeman 2014b), and during species introductions (e.g., Peterson 2011; Petitpierre et al. 2012). Given that phylogenetic niche conservatism appears to be pervasive, how do closely related tropical taxa diverge to inhabit different elevational zones?

This question can be explored by identifying the non mutually exclusive ecological and evolutionary forces that could override niche conservatism and drive elevational divergence. Because speciation is typically allopatric (e.g., for birds; Barraclough and Vogler 2000; Price 2008), instances of elevational divergence between related species found along the same mountain slope result from successful range expansions that bring species into secondary contact following allopatric speciation. There are three processes that could generate such elevational divergence (Fig. 1). First, elevational divergence may simply be a stochastic process correlated with the amount of time that has passed since species last shared a common ancestor. Elevational divergence among closely related taxa may be opposed by stabilizing selection, gene flow and the genetic constraint of shared evolutionary history, with the probability of divergence increasing with greater evolutionary time (reviewed in Wiens et al. 2010). This stochastic model of elevational divergence therefore predicts that more closely related species should have more similar elevational distributions than distantly related species. Additionally, this model predicts that variance in elevational divergence should increase with genetic distance when comparing closely related species, such that few species should have low genetic distances and high elevational divergence (i.e. a scatterplot of genetic distance vs. elevational divergence would exhibit a triangular distribution). Because range expansions following allopatric speciation are necessary to lead to sympatry (defined here as two species found along the same mountain slope), sympatric species tend to be older than allopatric species (Weir and Price 2011; Pigot and

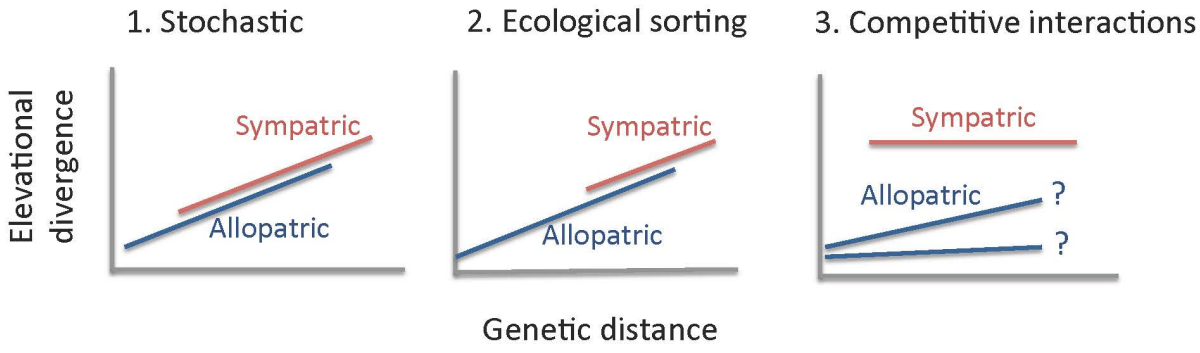
Tobias 2013; Price et al. 2014; Tobias et al. 2014). Thus, a purely stochastic model predicts that, due to the greater average evolutionary age of sympatric species, elevational distributions should be more divergent in sympatric species than allopatric species (Tobias et al. 2014; Fig. 1).

Second, ecological interactions during secondary contact may act as a sorting mechanism permitting species that have evolved sufficiently divergent elevational distributions in allopatry to successfully attain sympatry following secondary contact (Cadena 2007, see Fig. 1). The ecological sorting hypothesis parallels the stochastic hypothesis in assuming elevational divergence generally increases with evolutionary time, but differs in positing that a deterministic mechanism influences the likelihood that sister species become sympatric upon secondary contact. Specifically, the sorting model assumes that competition based on "limiting similarity" prevents sympatry between sister species with similar elevational distributions when range expansions bring them into secondary contact but allows sympatry between sister species if their elevational distributions have diverged sufficiently while in allopatry (Cadena 2007; Pigot and Tobias 2013). Because the elevational divergence that allows sister species to become sympatric in the sorting hypothesis becomes more likely to evolve with increasing evolutionary time, the sorting hypothesis also predicts that greater elevational divergence in sympatric species is primarily explained by their greater evolutionary age.

Third, competitive interactions upon secondary contact may drive elevational divergence between closely related species (Diamond 1973, see Fig. 1). While the ecological sorting hypothesis proposes that competition in secondary contact sorts pre-existing divergence, the competitive interactions hypothesis proposes that competitive interactions in secondary contact actively drive divergence. For example, the negative impact of strong interference interspecific competition between sister taxa in secondary contact could drive spatial segregation to reduce

interspecific interactions (Diamond 1973). Equally, apparent competition mediated by species-specific predators or pathogens could cause closely-related, ecologically similar species to partition elevational space upon secondary contact (Ricklefs 2010). Similar to the first two hypotheses, the competition hypothesis predicts that elevational distributions should be more divergent in sympatric species than allopatric species. However, it differs by predicting that geographic overlap (i.e., sympatry vs. allopatry) and not evolutionary age explains elevational divergence (Fig. 1).

**Figure 1.** Three evolutionary processes to explain elevational divergence predict different relationships for how elevational divergence evolves over time in sympatric and allopatric sister species. All three processes assume that speciation is allopatric. Importantly, all three hypotheses predict that sympatric sister species have greater elevational divergence than allopatric sister species. The stochastic and sorting hypotheses predict that this difference is due to the older age of sympatric sister species, and that rates of elevational divergence are similar in allopatry and sympatry. The sorting hypothesis additionally predicts that only sister species with relatively high elevational divergence will successfully attain sympatry, while those with relatively low elevational divergence will remain allopatric. In contrast to the stochastic and sorting hypotheses, the competitive interactions hypothesis predicts that elevational divergence is explained by geographical overlap, with sympatric sister species tending to have higher elevational divergence than allopatric sister species regardless of genetic distance. In the competitive interactions hypothesis, elevational divergence in allopatry may either increase with genetic distance or remain low, depending on the strength of phylogenetic niche conservatism.



I tested the predictions of these hypotheses using data on sister species of birds found in the humid tropical mountains of three regions that are largely biogeographically independent—the Neotropics, the Himalayas and New Guinea. Although elevational specialization is observed in many tropical taxa (e.g., mammals: Patterson et al. 1998; butterflies: Hall 2005), birds are the only large group with both published, high-quality, range-wide elevational distribution data and many species-level phylogenies available for multiple geographic montane regions. They therefore provide a suitable taxonomic focus for investigating this question. Explaining tropical montane megadiversity requires understanding elevational specialization; while previous research has investigated this question for specific case examples, I conducted the first broad comparative analysis to test the evolutionary mechanisms that drive elevational divergence in tropical birds in multiple independent geographic regions.

**METHODS**

I used a sister species approach to evaluate hypotheses explaining elevational divergence in tropical montane avifaunas of three regions: the Neotropics, the Himalaya and New Guinea. The evolution of elevational distributions could be profitably explored with other phylogenetic approaches, such as using closely related groups of species as the unit of analysis (e.g., Weir and Price 2011). Because most elevational replacements are not sister taxa (Patton and Smith 1992; Cadena 2007), such an approach could potentially bias results towards the competitive interactions hypothesis. I used sister species as my unit of analysis in order to avoid such problems, and also to make unbiased comparisons of genetic distances between allopatric and sympatric sister species.

I identified sister species by performing a thorough survey of published molecular phylogenies of landbirds resident in the Neotropics, the Himalaya, and New Guinea, three tropical montane regions with diverse avifaunas. Most phylogenies were inferred from a combination of mitochondrial and nuclear markers, though a small number of older studies using mitochondrial data alone were included. When multiple phylogenies were available for the same clade, I used the most recent study to infer sister species relationships.

To minimize erroneous classification of sister species, I only considered molecular phylogenies that sampled >80% of species within a genus. A small number of well-sampled phylogenies identified members of different genera as sister species ($n$= 15). Given the relative lack of published phylogenetic information for New Guinean birds, I additionally included species from New Guinea genera that contain only two species ($n$= 13) as sister species. The aim of this study was to investigate elevational divergence in species inhabiting humid tropical mountains where climatic differences between regions are relatively small (as opposed to arid mountains; McCain 2009). I therefore used regional reference volumes (e.g., Stotz et al. 1996; Robson 2008; Beehler et al. 1986) to restrict my analysis to sister species where both taxa inhabit primarily humid climates. While the majority of sister species-pairs in my database were restricted to montane distributions, I also included species-pairs where one species is montane and the other found primarily in lowland environments.

*Elevational divergence*

I calculated elevational divergence between sister species pairs based on the species with the narrower elevational distribution. Elevational divergence was the proportion of this species' elevational distribution that overlapped with the elevational distribution of its sister species. This

metric ranged from 0, where the elevational distribution of the species with the smaller elevational range was entirely subsumed within the broader elevational range of its sister species, to 1, where sister species occupied non-overlapping elevational distributions. Species with wide distributions in humid Neotropical mountains typically occupy consistent elevational zones across the latitudinal gradient (Graves 1988; Stotz et al. 1996). Therefore, I assigned elevational distributions at the range-wide level for all species, using single sources for each region (New Guinea: Beehler et al. 1986; Himalayas: Del Hoyo et al. 1992; Neotropics: Stotz et al. 1996). For a small number of species described after the publication of these single sources (e.g. Coopmans and Krabbe 2000), I garnered elevational distribution data from field guides (e.g., Ridgely and Greenfield 2001).

Measuring elevational distributions at the range-wide level does not account for sister species that occupy divergent elevational distributions where they are sympatric but expanded distributions where they are allopatric (e.g., Diamond 1973; Remsen and Graves 1995, ~13 examples in my database). These case studies constitute the best distributional evidence that competitive interactions in secondary contact may drive elevational divergence (Diamond 1973; Diamond 1986). However, my approach classifies such cases as sympatric sister species with low elevational divergence, biasing my analysis against the competitive interactions hypothesis. It would be optimal to compare elevational distributions of sympatric species in both the sympatric and allopatric portions of their distributions when applicable. However, doing so would require elevational distribution information gathered at a local scale (e.g. single mountain or mountain range) that simply does not exist for many regions. I therefore followed the conservative course of using single reference volumes to measure elevational distributions at the range-wide level.

*Geographical overlap*

I used digital distribution maps (Ridgely et al. 2003) and regional field guides (Beehler et al. 1986; Del Hoyo et al. 1992; Ridgely and Tudor 2009) to assign sister species to two categories of geographical overlap: allopatric or sympatric. Allopatric sister species inhabited completely non-overlapping geographic distributions. Typically, allopatric sister species in my database inhabited distinct montane regions separated by lowland barriers. In contrast, I classified sister species present on the same mountain slope as sympatric. This designation therefore included sister species with both widespread and minimal (i.e., parapatric) elevational overlap. While analyses considering geographic range overlap as a quantitative trait could also be used to investigate elevational divergence, pervasive asymmetries in range sizes would likely obscure any possible relationship between geographical overlap and elevational divergence (e.g., even species with nearly identical elevational distributions in sympatry often differ markedly in their overall range size and would thus be categorized as having low range overlap). Moreover, the key question addressed in this study is whether sister species that likely interact ecologically over relatively short time scales (i.e., are present on the same mountain slope; Price et al. 2014) differ in elevational divergence from geographically isolated (allopatric) sister species that do not interact ecologically. Thus, I used "allopatric" and "sympatric" as the sole categories of geographical overlap for analyses.

*Genetic distances*

I obtained homologous mitochondrial DNA sequences from GenBank for most sister species. I then calculated uncorrected sequence divergence (p-distances) between sister species in MEGA5

(Tamura et al. 2011). Mitochondrial DNA sequences have been considered to represent neutral loci that evolve in a relatively clock-like fashion (Weir and Schluter 2008). If so, these measures of sequence divergence serve as a proxy for time since sister species last shared a common ancestor. Recent evidence that suggests mitochondrial DNA sequences may not necessarily be neutral loci (Dowling et al. 2008; Ribeiro et al. 2011) calls into question the assumption that mitochondrial divergence is an accurate proxy for time. Nevertheless, because there is no *a priori* expectation that rates of mitochondrial divergence differ between allopatric and sympatric sister species of tropical montane birds, my analysis should be robust to the assumption that mitochondrial DNA sequences are selectively neutral. However, limited introgression upon secondary contact could lead to a systematic reduction in the genetic distances of sympatric sister species relative to allopatric sister species. The majority of sympatric sister species in my database have relatively large divergences in mtDNA (e.g., fewer than 10% of the sympatric sister species in my analysis have genetic distances < 3%) and these closely related sympatric sister species tend to have low degrees of elevational divergence. While introgression may have occurred in some cases included in my analysis, dealing with introgression is beyond the scope of this paper, and there is no clear post-hoc method to identify which sister species in my database may have hybridized upon secondary contact.

*Statistical analysis*

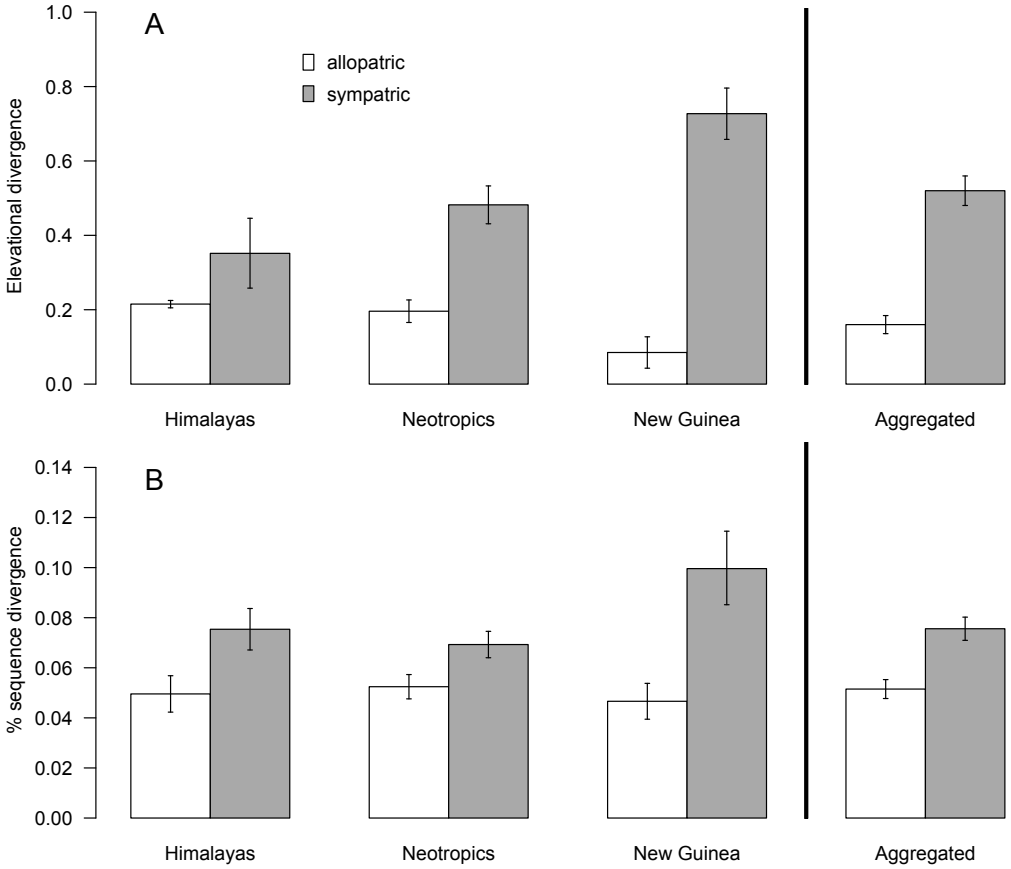
I used linear regression models and AICc-based model selection to test hypotheses to explain elevational divergence in sister species pairs. I developed a complete set of models to predict elevational divergence, with genetic distance, geographical overlap (sympatry or allopatry), and region (Neotropics, Himalayas and New Guinea) as predictor variables. I considered all

interaction terms between these predictor variables, and used AICc scores to select the best-supported model, using the "MuMIn" package in R to perform model selection and model averaging (R Development Core Team 2014).

## RESULTS

The final database is deposited in the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.6qg3g (Freeman 2015), and includes information on 203 sister species pairs from 41 families (136 in Neotropics, 35 in Himalayas, and 32 in New Guinea). Of these, I obtained sequence data for 182 sister species pairs: 125 from the Neotropics, 34 from the Himalayas, and 23 from New Guinea. Sympatric sister species ($n$= 96) had significantly greater elevational divergence than allopatric sister species ($n$= 107; 0.52 ± 0.39 vs. 0.16 ± 0.25; Wilcoxon rank sum test: W = 2493, p-value= <0.0001, Fig. 2; summary statistics presented are mean ± sd). In addition, as expected given the dominance of allopatric speciation in birds (Price 2008), allopatric sister species ($n$= 99 with sequence data) had smaller genetic distances than sympatric sister species ($n$= 83 with sequence data; 0.052 ± .034 vs. 0.076 ± 0.041; Wilcoxon rank sum test: $W$ = 2785, $p$-value= 0.0001, Fig. 2). These patterns—that sympatric sister species are both older and more divergent in elevational distribution than allopatric sister species—are compatible with all three hypotheses. Thus, I used model results to test the different patterns of elevational divergence over time in allopatry and sympatry predicted by the different hypotheses (Martin et al. 2010; Pigot and Tobias 2013; Tobias et al. 2014, see Fig. 1).

**Figure 2.** Elevational divergence (*A*) and genetic distance (*B*) are both greater in sympatric than allopatric avian sister species in each montane region. Bars illustrate means ± standard errors. Elevational divergence is based on range-wide elevational distributions (Neotropics: *n*= 136, Himalayas: *n*= 35, New Guinea: *n*= 32), and genetic distance is measured as percent sequence divergence in mtDNA (Neotropics: *n*= 125, Himalayas: *n*= 34, New Guinea: *n*= 23). In all three regions, sympatric sister species have significantly higher elevational divergence and larger genetic distances than allopatric sister species.



The best model to predict elevational divergence contained three parameters (genetic distance, geographical overlap and a genetic distance × region interaction term; see Table 1). Because the second and third best-supported models had comparable AICc scores and relatively high model weights (Table 1), I used model averaging to combine the top three models into the final model (Table 2).

**Table 1.** Models to predict elevational divergence in tropical montane birds

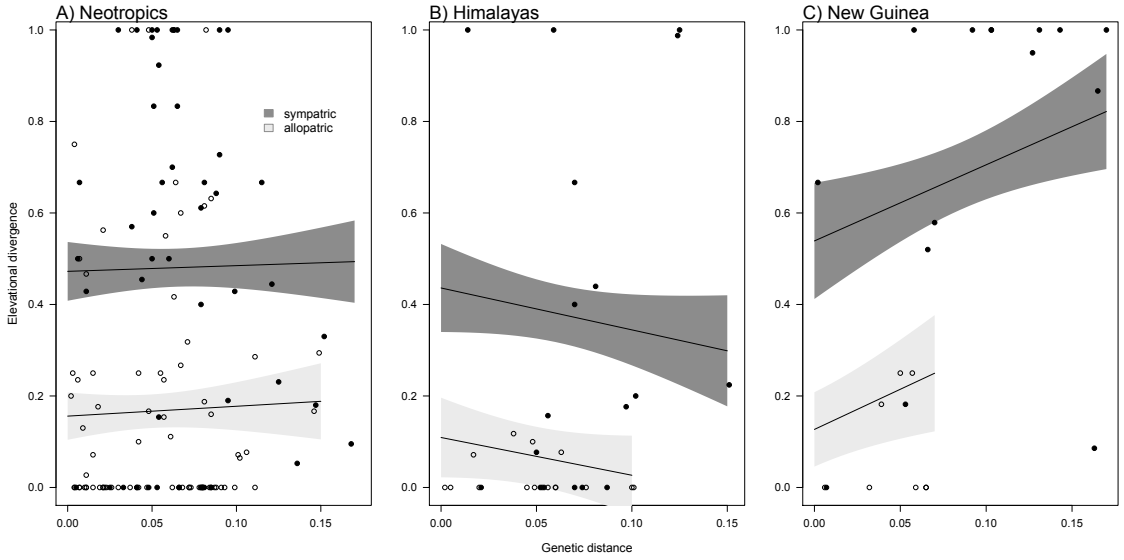
| Parameters in model | df | AICc | ΔAIC | Model weight |
|---|---|---|---|---|
| Genetic dist. + Geog. overlap + Genetic dist. × Region | 6 | 103.8 | 0 | 0.39 |
| Genetic dist. + Geog. overlap + Geog. overlap × Region | 8 | 105 | 1.27 | 0.20 |
| Genetic dist. + Geog. overlap + Genetic dist. × Geog. overlap + Genetic dist. × Region | 7 | 105.8 | 2.04 | 0.14 |
| Genetic dist. + Geog. overlap + Genetic dist. × Geog. overlap + Genetic dist. × Region + Geog. overlap × Region + Genetic dist. × Geog. overlap × Region | 11 | 106.7 | 2.91 | 0.09 |
| Genetic dist. + Geog. overlap + Genetic dist. × Geog. overlap + Geog. overlap × Region | 9 | 107.2 | 3.47 | 0.07 |
| Genetic dist. + Geog. overlap + Genetic dist. × Region + Geog. overlap × Region | 8 | 107.3 | 3.58 | 0.06 |
| Genetic dist. + Geog. overlap + Genetic dist. × Geog. overlap + Genetic dist. × Region + Geog. overlap × Region | 9 | 109.5 | 5.74 | 0.02 |
| Geog. overlap + Geog. overlap × Region | 7 | 109.9 | 6.1 | 0.02 |
| Genetic dist. + Geog. overlap | 4 | 111.6 | 7.84 | 0.01 |
| Genetic dist. + Geog. overlap + Genetic dist. × Geog. overlap | 5 | 113.5 | 9.75 | 0 |
| Geog. overlap | 3 | 122.7 | 18.95 | 0 |
| Genetic dist. + Genetic dist. × Region | 5 | 139.7 | 35.97 | 0 |
| Genetic dist. | 3 | 147.6 | 43.84 | 0 |

This final averaged model thus contained a geographical overlap × region interaction term as an additional parameter (Table 2). While the final averaged model contained the four parameters described above, the only significant predictor of elevational divergence was geographical overlap; sympatric sister species had significantly greater elevational divergence than allopatric sister species (Table 2, Fig. 3). In contrast, there was no effect of genetic distance on elevational divergence in the final averaged model (Table 2, Fig. 3). Importantly, these key results were robust to different approaches to model selection; whether I considered the top three models in isolation, the top two models combined in an average model, or the top three models combined in an averaged model as presented in Table 2, sympatry was the only significant predictor variable (p-values always $< 0.001$) and the genetic distance parameter was never significant (p-values ranging from 0.18 to 0.71). Though regions varied in the effect of genetic distance and geographical overlap on elevational divergence (Table 2, Figs. 2 and 3), the pattern of increased elevational divergence in sympatric sister species compared to allopatric sister species, regardless of genetic distance, was consistent across regions (Fig. 3).

**Table 2.** Final averaged model to predict elevational divergence between sister species of tropical montane birds. Approximate confidence intervals were calculated as the parameter estimate ± 2*std. error. P- values for parameter significance were calculated by MuMIn in R (R Development Core Team 2014) following model averaging.

| Parameter | Estimate | Std. Error | Approximate 95% conf. interval | z value | p-value |
|---|---|---|---|---|---|
| (Intercept) | 0.11 | 0.087 | -0.06 – 0.28 | 1.25 | 0.21 |
| Genetic distance | -0.83 | 1.16 | -3.15 – 1.49 | 0.71 | 0.48 |
| Geographical overlap (sympatric) | 0.33 | 0.081 | 0.17 – 0.49 | 4.01 | <0.0001 |
| Genetic distance × Region (New Guinea) | 2.59 | 1.84 | -1,09 – 6.27 | 1.41 | 0.16 |
| Genetic distance × Region (Neotropics) | 1.04 | 0.98 | -0.92 – 3.05 | 1.06 | 0.29 |
| Geographical overlap (allopatric) × Region (Neotropics) | 0.047 | 0.088 | -0.13 – 0.22 | 0.53 | 0.60 |
| Geographical overlap (sympatric) × Region (Neotropics) | 0.036 | 0.074 | -0.11 – 0.18 | 0.49 | 0.63 |
| Geographical overlap (allopatric) × Region (New Guinea) | 0.018 | 0.077 | -0.14 – 0.17 | 0.23 | 0.82 |
| Geographical overlap (sympatric) × Region (New Guinea) | 0.010 | 0.17 | -0.33 – 0.35 | 0.59 | 0.56 |
| Genetic distance × Geographical overlap (sympatric) | -0.009 | 0.62 | -1.25 – 1.23 | 0.15 | 0.89 |

**Figure 3.** Model predictions show greater elevational divergence in sympatric than allopatric sister species of tropical montane birds over a range of genetic distances in (*A*) the Neotropics, (*B*) Himalayas and (*C*) New Guinea. Trendlines show predictions of the final averaged model presented in Table 2, with standard error shaded. Raw data are plotted as filled (sympatric sister species-pairs) or open (allopatric sister species-pairs) circles. Because the final averaged model did not include a region x geographical overlap parameter, the slopes for sympatric and allopatric sister species within a single region are parallel. Model predictions are illustrated over the range of genetic distances present in the data for each region and category of geographical overlap.




## DISCUSSION

My results support the hypothesis that competitive interactions upon secondary contact drive elevational divergence in tropical montane avifaunas. I found that elevational divergence between sister species of tropical montane birds in the Neotropics, the Himalaya and New Guinea is predicted by geographical overlap and not by genetic distance—sympatric sister species had greater elevational divergence than allopatric sister species regardless of genetic distance (Fig. 3, Table 2). This result demonstrates that sympatry is often required to generate elevational divergence between sister species, consistent with predictions of the competitive interactions hypothesis.

In contrast, this result is not consistent with the stochastic and ecological sorting hypotheses, which both predict that elevational divergence is largely a function of evolutionary age. The stochastic and ecological sorting hypotheses also predict that examples of sister species with high elevational divergence but low genetic distances should be rare, yet there are many such examples in my dataset. In addition, the ecological sorting hypothesis assumes that the niche differences that eventually permit sympatry evolve in allopatry. However, elevational distributions in allopatric sister species diverged minimally even at large genetic distances (Fig. 3). Hence, elevational distributions that evolved in allopatry do not appear to provide much variation that could be sorted upon for tropical montane birds, at least when considering the database of sister species I used. Thus, the geographically replicated patterns I found are most consistent with the hypothesis that competitive interactions upon secondary contact drive divergence in elevational distributions between sister species of tropical montane birds.

However, it is important to recognize that ecological sorting could generate the observed patterns if range expansions are assumed to be highly probable at all times. In this scenario, range expansions are sufficiently frequent that sister species that evolve divergent elevational distributions in allopatry soon undertake range expansions that lead to successful sympatry, explaining why sister species with divergent elevational distributions tend to be sympatric regardless of evolutionary age. The flip side to this scenario is that range expansions that brought sister species inhabiting similar elevational distributions into secondary contact would be both frequent and unsuccessful, and such sister species would remain allopatrically distributed. While the ecological sorting hypothesis likely applies to specific case examples of tropical montane birds (e.g.,

Cadena 2007), the assumption that range expansions that lead to secondary contact are equally high for all species is unlikely to be true for tropical birds. Instead, geographic and behavioral barriers to dispersal likely limit the probability of range expansions in tropical birds (Price 2008; Burney and Brumfield 2009; Weir and Price 2011; Salisbury et al. 2012; Smith et al. 2014).

My results demonstrate that elevational divergence in tropical montane birds is driven by a factor that affects sympatric sister species but not allopatric sister species. Competitive interactions that occur during secondary contact, such as interference interspecific competition (Diamond 1973) and apparent competition driven by species-specific predators and parasites (Holt and Lawton 1994; Ricklefs 2010), are likely processes that could drive elevational divergence between sister species of tropical montane birds. Resource competition between avian sister species upon secondary contact is expected to be intense due to high dietary niche overlap (Price 2008). Case studies of "natural experiments," where species inhabit broader elevational distributions in the absence of a congener, are consistent with the hypothesis that interspecific competition influences elevational distributions of tropical montane birds (Diamond 1973; Terborgh and Weske 1975; Diamond 1986; Cadena and Loiselle 2007). In contrast, the possibility that species-specific enemies (predators and parasites) drive elevational divergence has not been rigorously tested, though a recent review of the causes of species' warm-edge limits did not find any case examples where these range limits were set by pathogens (Cahill et al. 2014). Further research testing the processes that drive elevational divergence in particular case studies of sympatric tropical montane birds (or

other taxa) are necessary to fully evaluate mechanisms underlying the competitive interactions hypothesis.

The interpretation that competition drives elevational divergence rests on the assumption that allopatric speciation, not parapatric speciation (e.g., Patton and Smith 1992; Smith et al. 1997), is the dominant geographic mode of speciation in tropical montane birds. Applied to elevational gradients, parapatric speciation models propose that an ancestral species with a broad elevational distribution speciates *in situ* into low- and high-elevation species that are sister species inhabiting divergent elevational distributions. Parapatric speciation could thus explain why sympatric sister species inhabit divergent elevational distributions regardless of elevational age. However, molecular studies of species thought to be likely candidates for parapatric speciation typically reveal that reproductive isolation evolved in allopatry (e.g., Cadena 2007; Fuchs et al. 2011). Given that the primacy of allopatric speciation in birds is well established (Barraclough and Vogler 2000; Price 2008; Pigot and Tobias 2013; Price et al. 2014), it seems unlikely that parapatric speciation is sufficiently common to be an important driver of observed patterns of elevational divergence in my database.

In conclusion, my results support the hypothesis that competitive interactions upon secondary contact are a common mechanism driving elevational divergence in tropical montane birds. While varying scenarios may explain elevational divergence in specific case examples, I found broad support for the competitive interactions hypothesis in a diverse range of taxa in each of three geographically and phylogenetically independent avifaunas, suggesting the competitive interactions hypothesis may apply broadly to community assembly in tropical montane avifaunas. By driving the niche

divergence that allows related species to occur sympatrically, competitive interactions may play a creative role in the assembly of diverse communities along elevational gradients (Schluter 2000). Future tests with additional taxonomic groups across a range of latitudes can test the generality of this model of community assembly.

**ACKNOWLEDGMENTS**

W. Hochachka provided statistical assistance. The Lovette lab, D. Ackerly, A. Agrawal, C. D. Cadena, S. Freeman, R. Ricklefs, N. Senner, J. A. Tobias, the PhyloFun group and four anonymous reviewers provided comments that greatly improved this manuscript. BGF was supported by a graduate fellowship from the Cornell Lab of Ornithology. This material is based upon work supported by the National Science Foundation Graduate Research Fellowship under Grant No. 2011083591.

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CHAPTER 5

# INTERSPECIFIC AGGRESSION BETWEEN NEW GUINEAN SONGBIRD ELEVATIONAL REPLACEMENTS IS LINKED TO DISTRIBUTIONAL OVERLAP

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**ABSTRACT**

In tropical avifaunas, a common pattern is for closely related species to "replace" one another along an elevational gradient. A longstanding hypothesis is that interspecific aggression between species-pairs of elevational replacements influences their elevational limits, but empirical data testing this hypothesis remains scarce. We used reciprocal playback experiments to measure interspecific aggression in five species-pairs of New Guinean elevational replacements. We documented interspecific aggression in three species-pairs that had zones of elevational overlap where both species were present, but not in two species-pairs that had narrow "no man's land" gaps between their elevational distributions. When present, interspecific aggression was always strongest at the lower elevation species' leading range margin, suggesting interspecific aggression is a learned response to the presence of a competitor. In each of these three species-pairs, interspecific aggression was asymmetric—the lower elevation species was more

aggressive towards the upper elevation species than vice versa. These results support the hypothesis that asymmetric interspecific aggression is one factor influencing elevational limits of New Guinean elevational replacements.

## INTRODUCTION

Tropical mountains are the most biodiverse terrestrial environments on Earth (Myers et al. 2000) Tropical montane hyperdiversity results in large part from the fact that tropical montane species typically inhabit narrow elevational distributions (Patterson et al. 1998, McCain 2009,), and one common pattern of elevational specialization is for closely related species to "replace" one another along elevational gradients. Elevational replacements are common in a variety of tropical montane taxa (e.g., bats: Patterson et al. 1998, butterflies: Hall 2005, lizards: Bell et al. 2010, dung beetles: Larsen 2012,), and have been especially studied in songbirds (Terborgh and Weske 1975, Remsen and Graves 1995). However, the abiotic and biotic factors that explain why species-pairs of elevational replacements inhabit parapatric elevational distributions remain uncertain (Jankowski et al. 2012).

One historically popular hypothesis posits that interference interspecific competition is an important factor limiting the elevational distributions of elevational replacements (Diamond 1973, Terborgh and Weske 1975). In territorial species, interference interspecific competition is often mediated by interspecific aggression (Peiman and Robinson 2010, Grether et al. 2013), and one prediction of the interspecific competition hypothesis is that territorial elevational replacements interact aggressively where their elevational distributions overlap. Supporting this hypothesis, field

experiments have documented interspecific aggression in case studies of elevational replacements of Neotropical songbirds (Jankowski et al. 2010, Caro et al. 2013) and rodents (Pasch et al. 2013), though the extent to which species-pairs of elevational replacements interact aggressively where their distributions overlap remains uncertain.

Elevational replacements are particularly prominent in the New Guinean avifauna, and "natural experiments"—where a species expands its elevational distribution in the absence of its elevational replacement (putative competitor)—are consistent with the hypothesis that interspecific competition limits elevational limits in these species-pairs (Diamond 1973). The interspecific competition hypothesis predicts that i) species-pairs show interspecific aggression, and ii) that interspecific aggression should be strongest at species elevational limits where they interact (e.g., in the zone of elevational overlap where both species occur and interact). We tested these predictions by using reciprocal playback experiments to measure interspecific aggression in five species-pairs of territorial New Guinean songbird elevational replacements.

## METHODS

### Focal species

We studied five species-pairs of territorial insectivorous bird species that are elevational replacements within their New Guinean distribution (Beehler et al. 1986). All species are common understory residents on the northwest ridge of Mt. Karimui, Chimbu Province, Papua New Guinea, originally surveyed by J. Diamond (1972) in 1965 and resurveyed in 2012 by B.G.F. and A.M.C.F. (Freeman and Class Freeman 2014a, b). The elevational replacements we studied were a quartet of understory robins representing three species-

pairs of elevational replacements (lowland White-rumped Robin *Peneothello bimaculatus*, foothill White-eyed Robin *Pachycephalopsis poliosoma*, montane Slaty Robin *Peneothello cyanus* and upper montane White-winged Robin *Peneothello sigillatus*), a species-pair of terrestrial jewel-babblers (foothill Chestnut-backed Jewel-babbler *P. castanonota* and montane Spotted Jewel-babbler *P. leucosticta*), and a species-pair of understory fantails (montane Black Fantail *Rhipidura atra* and upper montane Dimorphic Fantail *R. brachyrhynca*) (Tables 1 and 2). These species-pairs vary in their degree of elevational overlap on New Guinean mountainslopes, with sharp parapatric borders reported for most species-pairs (jewel-babblers and understory robins) and relatively larger zones of elevational overlap in fantails (Diamond 1973, BGF pers. obs.).

**Playback Experiments**

We conducted playback experiments in October-December 2012. We first compiled a collection of locally recorded natural vocalizations ($n$ = 6-15 songs per species) using a Marantz PMD661 Field Recorder and a Sennheiser MKH 70 directional microphone. We arbitrarily selected the specific recordings used in particular playback trials to minimize pseudoreplication. Recordings have been archived at the Macaulay Library of Natural Sounds, Cornell Lab of Ornithology.

We conducted playback experiments on active territories of all elevational replacements across a range of elevations (Table 1). We considered singing individuals to be actively defending territories, and mapped the location of singing individuals with a Garmin 62S GPS. We initiated playback experiments by placing a Pignose amplifier (hereafter 'speaker') at the marked location. The speaker was attached to an iPod via a 20

m audio cable, and we broadcast song stimuli and observed the behavioral response (if any) of the territory owner(s) while hiding behind vegetation ~15 m from the speaker to minimize the influence of our physical presence. We completed playback experiments between 06:15 h and 13:00 h, avoiding periods of moderate or heavy rain.

**Table 1.** Number of playback trials conducted for each species in all five species-pairs of elevational replacements. For each species-pair of elevational replacements, the upper elevation species is listed above its lower elevation replacement. Within a species-pair, we report the number of playback trials and the elevational zone in which playback experiments occurred for each species. White-eyed and Slaty Robins each appear as the lower elevation species in one species-pair of elevational replacements and the upper elevation species in a second species-pair of elevational replacements.

| Species-pair | Species | Playback trials | Elevation of playbacks (m.a.s.l) |
|---|---|---|---|
| Slaty/White-winged Robin | White-winged Robin | 9 | 2,325 – 2,505 |
| | Slaty Robin | 9 | 1,872 – 2,143 |
| White-eyed/Slaty Robin | Slaty Robin | 16 | 1,673 – 1,965 |
| | White-eyed Robin | 19 | 1,448 – 1,693 |
| White-rumped/White-eyed Robin | White-eyed Robin | 19 | 1,240 – 1,411 |
| | White-rumped Robin | 23 | 1,042 – 1,282 |
| Chestnut-backed/ Spotted Jewel-babbler | Spotted Jewel-babbler | 17 | 1,514 – 2,142 |
| | Chestnut-backed Jewel-babbler | 15 | 1,242 – 1,455 |
| Black/Dimorphic Fantail | Dimorphic Fantail | 13 | 2,050 – 2,520 |
| | Black Fantail | 19 | 1,722 – 2,520 |

Playback experiments consisted of control, conspecific, and heterospecific trials (because elevational replacements of understory robins represent two genera, we term these trials "heterospecific" instead of "congeneric"). We began experiments with the control trial of three minutes of playback of a locally common species unlikely to compete with the territory owner (e.g. *Pachycephala* whistlers), followed by five minutes of behavioral observation. We next performed conspecific and heterospecific trials (three minutes of playback followed by five minutes of behavioral observation for each trial), alternating their relative order (conspecific trial first vs. heterospecific trial first) between experiments. The conspecific trial tested the focal species' behavioral response to playback of its own species, while the heterospecific trial tested the focal species' behavioral response to playback of its elevational replacement. All trials for a given territory were performed sequentially in a single 24-minute session, though we used an expanded time period of behavioral observation (eight minutes in lieu of five) for jewel-babblers to accommodate their delayed behavioral response to playback.

We quantified four behavioral responses to playback: closest approach to speaker (m) (hereafter "closest approach"), latency to approach speaker (s), latency of vocal response (s), and number of vocalizations. All focal species are relatively shy and infrequently seen (Beehler et al. 1986), and there were no cases where we visually observed an individual prior to initiating a playback trial. We measured latency to approach as the time elapsed prior to the first observed approach to within 15 m of the speaker, and closest approach as a continuous variable bounded by 0 (if the responding bird perched on the speaker) and 15 m (due to dense understory vegetation, the maximum distance we could reasonably detect a territory owner approaching the speaker). We

estimated closest approach by eye during the course of playback experiments and checked our visual estimates by later pacing off the distance between the speaker and location of the responding bird's closest approach. Finally, we measured latency to vocal response as the first vocalization (call or song) given by the focal individual/pair at any distance from the speaker after initiating a playback trial.

Birds always responded aggressively to conspecific playback, with at least one individual approaching the speaker during conspecific trials. However, territory owners often did not respond to heterospecific trials and typically did not respond to control playback trials. We categorized the closest approach of these non-responders as 15 m (see above) and their latency to approach speaker and vocal response as the summed duration of playback trials and behavioral observation periods (e.g., 480 s for non-jewel-babbler trials).

**Elevational limits**

We measured species' elevational limits in October-November 2012 using point counts and observations along Mt. Karimui's northwestern ridge. Briefly, one observer familiar with vocalizations of New Guinean birds (B.G.F.) conducted five-minute point counts at 33 sites located along an elevational transect stretching from 1,330 m.a.s.l. (meters above sea level) to 2,520 m.a.s.l. Point count sites were located at least 150 m apart, and were visited on each of three mornings (06:00 h – 12:00 h). We used point count data to roughly estimate species' elevational limits, then conducted extensive observational fieldwork at elevations near species' estimated elevational limits to locate territories of focal species for future playback experiments and to determine species' elevational limits

at a fine spatial scale. We found narrow zones of elevational overlap in two cases (White-rumped/White-eyed Robin and White-eyed/Slaty Robin), a larger zone of elevational overlap in one case (Black/Dimorphic Fantail), and narrow "no man's land" gaps between species' elevational distributions in the final two cases (Slaty/White-winged Robin and Chestnut-backed/Spotted Jewel-babbler, see Table 2). We note that species' abundance distributions were not necessarily uniform. In particular, while Black and Dimorphic Fantails co-occurred over a wide swath of montane elevations (Table 2), Black Fantails were abundant at middle elevations where Dimorphic Fantails were absent but markedly more scarce at high elevations where Dimorphic Fantails were relatively common (B.G.F. personal observation).

**Table 2.** Elevational distributions of species at the study site measured in October-November 2012.

| Species | Elevational distribution (m) |
|---|---|
| White-rumped Robin | <1,000 to 1,282 |
| White-eyed Robin | 1,240 – 1,693 |
| Slaty Robin | 1,673 – 2,158 |
| White-winged Robin | 2,325 – 2,520 |
| Chestnut-backed Jewel-babbler | <1,000 – 1,458 |
| Spotted Jewel-babbler | 1,508 – 2,142 |
| Black Fantail | 1,330 – 2,520 |
| Dimorphic Fantail | 2,050 – 2,520 |

**Statistical analysis**

We conducted all statistical analyses in R (R Development Core Team 2014). Because we were interested in behavioral interactions between pairs of species that are elevational replacements, we constructed separate models for each species-pair of elevational replacements. For each species-pair, we used a principal components analysis (PCA) to collapse all four behavioral response variables from playback trials into a single variable that summarized aggressive response (Benites et al. 2014, Reif et al. 2015). In each case, behavioral response variables that indicated greater aggression (closer approaches, faster approaches, faster vocal responses and greater number of vocalizations) loaded positively on PC1, which explained a high percentage (72-79%) of variance in the data for each species-pair (Table 3). We then constructed linear mixed models to analyze behavioral responses to playback, using PC1 values as our response variable.

**Table 3**. PC1 variance and loadings for each species-pair. For all species, the first principal component explained a large majority of variance in the raw measurements, and all of the measured facets of aggression loaded onto the first principal axes such that PC1 scores represent an appropriate measure of aggression in response to playback.

| Species-pair | PC1 | Closest approach | Latency approach | Latency vocalize | Number of vocalizations |
|---|---|---|---|---|---|
| White-rumped/White-eyed Robin | 73.5% | -0.53 | -0.54 | -0.46 | 0.46 |
| White-eyed/Slaty Robin | 72.6% | -0.54 | -0.53 | -0.49 | 0.43 |
| Slaty/White-winged Robin | 74.7% | -0.55 | -0.55 | -0.49 | 0.39 |
| Chestnut-backed/Spotted Jewel-babbler | 78.1% | -0.53 | -0.49 | -0.51 | 0.46 |
| Black/Dimorphic Fantail | 78.9% | -0.52 | -0.54 | -0.49 | 0.43 |

We included the following fixed predictor variables in each model: 1) trial type (six categories: conspecific, heterospecific, and control trials for each species within a species-pair), 2) an interaction between trial type and elevation, and 3) order of playback trials for each species (conspecific first vs. heterospecific first). Using "trial type" as a fixed effect facilitates interpretation of model parameters and is statistically equivalent to an alternative formulation that includes species, trial, and a species × trial interaction instead of "trial type." To account for variation among individuals in their response to playback trials, we included territory as a random effect. We examined whether the order of playback trials influenced behavioral responses to playback by fitting models for each species-pair with and without an order term. Given our small sample sizes, we erred on the side of caution (against model overfitting) by using Bayesian Information Criterion (BIC) model selection (Burnham 2004) to evaluate whether models including the order term outperformed models lacking this predictor variable, and used the best-supported model (the model with the lowest BIC value) for further analysis. We defined interspecific aggression as cases where aggression scores in response to heterospecific trials were significantly larger than aggression scores in response to control trials, and used slope estimates of the trial type × elevation interaction to determine if aggression scores were significantly related to elevation. While our formal statistical tests are based on models with multiple fixed effects and a random effect, graphical presentations of these same results present regression lines from simple linear regressions to illustrate qualitatively identical patterns. The simplified linear regressions used for figures were needed because there is no generally agreed upon way of calculating confidence intervals

around predictions from mixed models, and we wanted our figures to provide illustrations of levels of statistical confidence in patterns.

**RESULTS**

In all cases, BIC values were lower for the simpler model lacking the order term (Table 4), indicating that the relative order of conspecific and heterospecific trials explained minimal variation in behavioral response to playback. Therefore, we only present results from the simpler, better-supported models (Tables 5-9).

**Table 4**. BIC model comparison of linear regression models for each species-pair.

| Species pair | Predictor variables | df | BIC | Δ BIC |
|---|---|---|---|---|
| White-rumped/White-eyed Robin | trial type + trial type × elevation | 14 | 331.36 | 0 |
| | trial type + trial type × elevation + order | 15 | 336.16 | 4.8 |
| White-eyed/Slaty Robin | trial type + trial type × elevation | 14 | 285.25 | 0 |
| | trial type + trial type × elevation + order | 15 | 287.13 | 1.88 |
| Slaty/White-winged Robin | trial type + trial type × elevation | 14 | 124.59 | 0 |
| | trial type + trial type × elevation + order | 15 | 128.54 | 3.95 |
| Chestnut-backed/Spotted Jewel-babbler | trial type + trial type × elevation | 14 | 240.98 | 0 |
| | trial type + trial type × elevation + order | 15 | 245.54 | 4.56 |
| Black/Dimorphic Fantail | trial type + trial type × elevation | 14 | 296.46 | 0 |
| | trial type + trial type × elevation + order | 15 | 300.62 | 4.16 |

**Table 5.** Parameter estimates with standard errors for fixed effects in White-rumped/White-eyed Robin mixed model. For the categorical "trial type," the factor level "White-eyed Robin heterospecific" is denoted as the intercept, and parameter estimates for other trial types describe deviations from this intercept value. Interpretation is more straightforward for trial type × elevation interaction terms: parameter estimates represent the estimated slope of this interaction.

| Predictor variable | Parameter | Estimate | Std. error |
|---|---|---|---|
| Trial type | (Intercept) | 12.86 | 0.87 |
| Trial type | White-eyed Robin conspecific | -10.55 | 1.23 |
| Trial type | White-eyed Robin control | 2.14 | 1.19 |
| Trial type | White-rumped Robin heterospecific | -1.53 | 1.13 |
| Trial type | White-rumped Robin conspecific | -10.16 | 1.13 |
| Trial type | White-rumped Robin control | 2.14 | 1.16 |
| Trial type × Elevation | White-eyed Robin heterospecific × Elevation | 0.012 | 0.012 |
| Trial type × Elevation | White-eyed Robin conspecific × Elevation | 0.015 | 0.012 |
| Trial type × Elevation | White-eyed Robin control × Elevation | -4.53e-18 | 0.014 |
| Trial type × Elevation | White-rumped Robin heterospecific × Elevation | 0.019 | 0.0061 |
| Trial type × Elevation | White-rumped Robin conspecific × Elevation | 0.0035 | 0.0061 |
| Trial type × Elevation | White-rumped Robin control × Elevation | -5.70e-19 | 0.0058 |

**Table 6.** Parameter estimates with standard errors for fixed effects in White-eyed/Slaty Robin mixed model. For the categorical "trial type" parameter, the factor level "Slaty Robin heterospecific" is denoted as the intercept, and parameter estimates for other trial types describe deviations from this intercept value. Interpretation is more straightforward for trial type × elevation interaction terms: parameter estimates represent the estimated slope of this interaction.

| Predictor variable | Parameter | Estimate | Std. Error |
|---|---|---|---|
| Trial type | (Intercept) | 13.66 | 0.70 |
| Trial type | Slaty Robin conspecific | -11.58 | 0.99 |
| Trial type | Slaty Robin control | 1.34 | 0.97 |
| Trial type | White-eyed Robin heterospecific | -2.89 | 1.034 |
| Trial type | White-eyed Robin conspecific | -5.59 | 1.034 |
| Trial type | White-eyed Robin control | 1.34 | 1.074 |
| Trial type × Elevation | Slaty Robin heterospecific × Elevation | 0.0057 | 0.0047 |
| Trial type × Elevation | Slaty Robin conspecific × Elevation | 0.0081 | 0.0047 |
| Trial type × Elevation | Slaty Robin control × Elevation | 3.14e-18 | 0.0049 |
| Trial type × Elevation | White-eyed Robin heterospecific × Elevation | 0.024 | 0.0059 |
| Trial type × Elevation | White-eyed Robin conspecific × Elevation | -0.014 | 0.0059 |
| Trial type × Elevation | White-eyed Robin control × Elevation | 0 | 0.0056 |

**Table 7.** Parameter estimates with standard errors for fixed effects in Slaty/White-winged Robin mixed model. For the categorical "trial type" parameter requires care, the factor level "Slaty Robin heterospecific" is denoted as the intercept, and parameter estimates for other trial types describe deviations from this intercept value. Interpretation is more straightforward for trial type × elevation interaction terms: parameter estimates represent the estimated slope of this interaction.

| Predictor variable | Parameter | Estimate | Std. Error |
|---|---|---|---|
| Trial type | (Intercept) | 15 | 0.75 |
| Trial type | Slaty Robin conspecific | -11.81 | 1.06 |
| Trial type | Slaty Robin control | -1.43e-15 | 1.13 |
| Trial type | White-winged Robin heterospecific | -1.87e-15 | 1.43 |
| Trial type | White-winged Robin conspecific | -10.2 | 1.43 |
| Trial type | White-winged Robin control | -9.52e-16 | 1.37 |
| Trial type × Elevation | Slaty Robin heterospecific × Elevation | -1.37e-17 | 0.0085 |
| Trial type × Elevation | Slaty Robin conspecific × Elevation | 0.016 | 0.0085 |
| Trial type × Elevation | Slaty Robin control × Elevation | 1.79e-17 | 0.0082 |
| Trial type × Elevation | White-winged Robin heterospecific × Elevation | -1.43e-19 | 0.0043 |
| Trial type × Elevation | White-winged Robin conspecific × Elevation | -1.06e-02 | 0.0043 |
| Trial type × Elevation | White-winged Robin control × Elevation | 5.73e-19 | 0.0043 |

**Table 8.** Parameter estimates with standard errors for fixed effects in Black/Dimorphic Fantail mixed model. For the categorical "trial type" parameter, the factor level "Black Fantail heterospecific" is denoted as the intercept, and parameter estimates for other trial types describe deviations from this intercept value. Interpretation is more straightforward for trial type × elevation interaction terms: parameter estimates represent the estimated slope of this interaction.

| Predictor variable | Parameter | Estimate | Std. error |
|---|---|---|---|
| Trial type | (Intercept) | 4.04 | 1.09 |
| Trial type | Black Fantail conspecific | -0.098 | 1.54 |
| Trial type | Black Fantail control | 10.96 | 1.56 |
| Trial type | Dimorphic Fantail heterospecific | 7.55 | 1.68 |
| Trial type | Dimorphic Fantail conspecific | -2.24 | 1.68 |
| Trial type | Dimorphic Fantail control | 10.96 | 1.71 |
| Trial type × Elevation | Black Fantail heterospecific × Elevation | 0.017 | 0.0025 |
| Trial type × Elevation | Black Fantail conspecific × Elevation | -0.0026 | 0.0025 |
| Trial type × Elevation | Black Fantail control × Elevation | 5.03e-19 | 0.0025 |
| Trial type × Elevation | Dimorphic Fantail heterospecific × Elevation | 0.0033 | 0.0055 |
| Trial type × Elevation | Dimorphic Fantail conspecific × Elevation | 0.00025 | 0.0055 |
| Trial type × Elevation | Dimorphic Fantail control × Elevation | -4.42e-19 | 0.0053 |

**Table 9.** Parameter estimates with standard errors for fixed effects in Chestnut-backed/Spotted Jewel-babbler mixed model. For the categorical "trial type" parameter, the factor level "Chestnut-backed Jewel-babbler heterospecific" is denoted as the intercept, and parameter estimates for other trial types describe deviations from this intercept value. Interpretation is more straightforward for trial type × elevation interaction terms: parameter estimates represent the estimated slope of this interaction.

| Predictor variable | Parameter | Estimate | Std. Error |
|---|---|---|---|
| Trial type | (Intercept) | 14.10 | 0.096 |
| Trial type | Chestnut-backed Jewel-babbler conspecific | -7.55 | 1.36 |
| Trial type | Chestnut-backed Jewel-babbler control | 0.91 | 1.42 |
| Trial type | Spotted Jewel-babbler heterospecific | 2.11 | 1.39 |
| Trial type | Spotted Jewel-babbler conspecific | -10.05 | 1.39 |
| Trial type | Spotted Jewel-babbler control | 0.91 | 1.33 |
| Trial type × Elevation | Chestnut-backed Jewel-babbler heterospecific × Elevation | 0.0069 | 0.0096 |
| Trial type × Elevation | Chestnut-backed Jewel-babbler conspecific × Elevation | 0.00068 | 0.0096 |
| Trial type × Elevation | Chestnut-backed Jewel-babbler control × Elevation | 1.26e-17 | 0.0092 |
| Trial type × Elevation | Spotted Jewel-babbler heterospecific × Elevation | -0.0066 | 0.0030 |
| Trial type × Elevation | Spotted Jewel-babbler conspecific × Elevation | -0.0019 | 0.0030 |
| Trial type × Elevation | Spotted Jewel-babbler control × Elevation | -9.57e-19 | 0.0027 |

We found interspecific aggression in the three species-pairs of elevational replacements that had zones of elevational overlap (White-rumped/White-eyed Robin, White-eyed/Slaty Robin, and Black/Dimorphic Fantail; Figures 1 and 2, Tables 5, 6 and 8), and did not find interspecific aggression in the two species-pairs of elevational replacements that did not have zones of elevational overlap (Slaty/White-winged Robin and Chestnut-backed/Spotted Jewel-babbler; Figure 3, Tables 7 and 9).

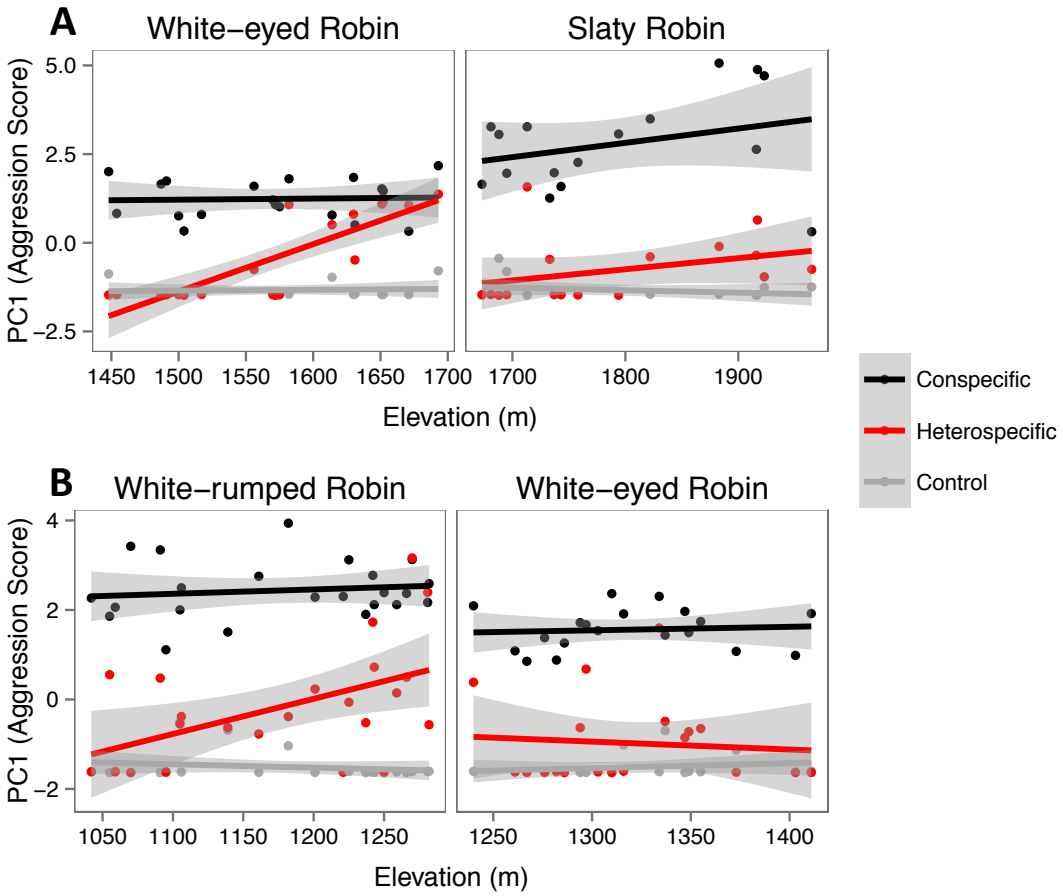


**Figure 1**. Aggression scores in response to playback trials in two species-pairs of understory robin elevational replacements that exhibit interspecific aggression: (**A**) White-rumped/White-eyed Robin and (**B**) White-eyed/Slaty Robin. Larger aggression scores indicate more aggressive responses to playback. For each species-pair, the lower elevation species is shown in the left column, and the upper elevation species in the right column; note that scales of the x-axes differ between columns (and species-pairs) to minimize the amount of uninformative white space. Trendlines with 95% confidence intervals are shown for each trial type, and raw data are also plotted. Trendlines and confidence intervals represent separate least squares regressions for each line, and are qualitatively similar to results from mixed models.

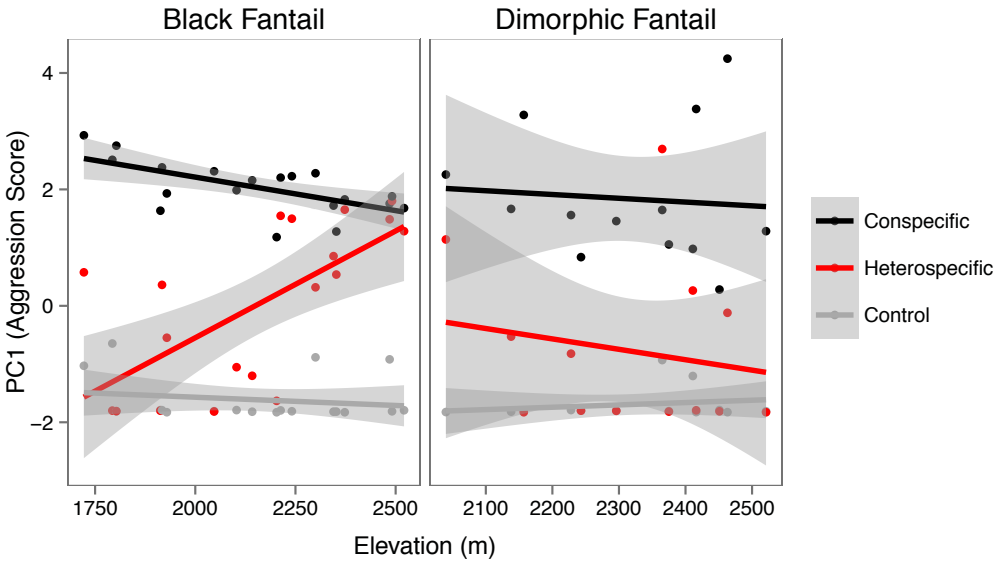


**Figure 2**. Aggression scores in response to playback trials for a pair of elevationally-replacing species of fantails that exhibits interspecific aggression: the lower elevation Black Fantail and upper elevation Dimorphic Fantail (in the left and right columns, respectively). Larger aggression scores indicate more aggressive responses to playback. Trendlines with 95% confidence intervals are shown for each trial type, and raw data are also plotted. Trendlines and confidence intervals represent separate least squares regressions for each line, and are qualitatively similar to results from mixed models.

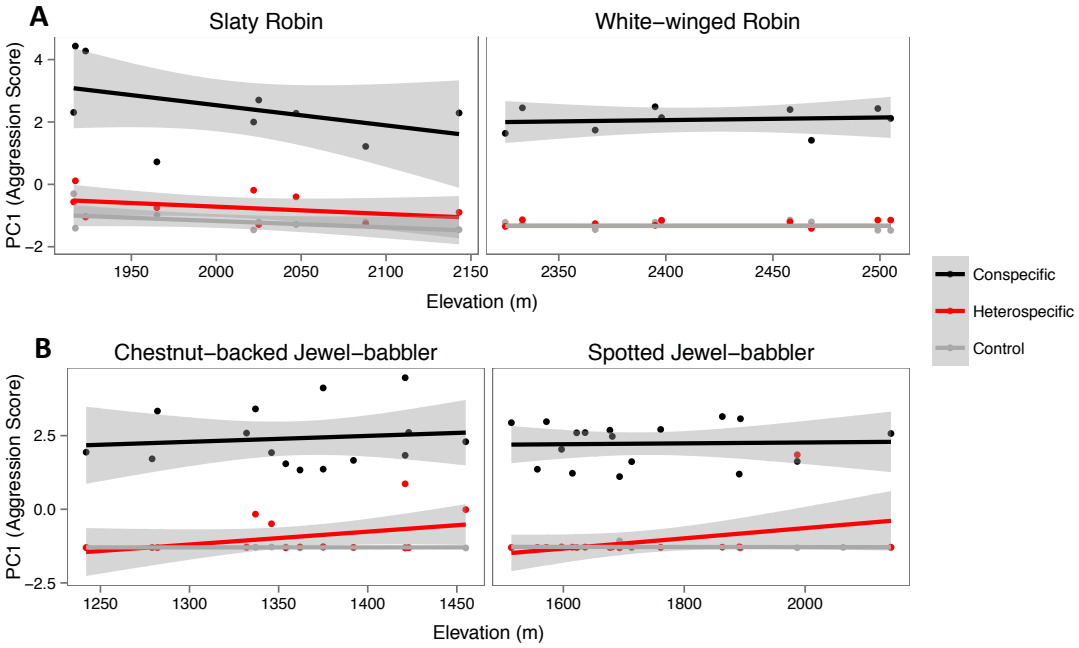


**Figure 3**. Aggression scores in response to playback trials in two species-pairs of understory elevational replacements that did not exhibit interspecific aggression: (**A**) Slaty/White-winged Robin and (**B**) Chestnut-backed/Spotted Jewel-babbler. Larger aggression scores indicate more aggressive responses to playback. For each species-pair, the lower elevation species is shown in the left column, and the upper elevation species in the right column—note that scales of the x-axes differ between columns (and species-pairs) to minimize the amount of uninformative white space. Trendlines with 95% confidence intervals are shown for each trial type, and raw data is also plotted. Trendlines and confidence intervals represent separate least squares regressions for each line, and are qualitatively similar to results from mixed models.

When present, interspecific aggression was asymmetric—the lower elevation species exhibited stronger interspecific aggression towards the upper elevation species than vice versa (Figures 1 and 2, Tables 5, 6 and 8). Interspecific aggression was also greatest at the lower elevation species' upper elevation limit, indicated by heterospecific trial × elevation interaction terms that were significantly positive for all the three lower elevation species that exhibited significant interspecific aggression (Figures 1 and 2, Tables 5, 6 and 8). The level of interspecific aggression at the lower elevation species' leading range margin varied among species-pairs (Figures 1 and 2). Models predicted that

White-rumped Robin aggression scores to heterospecific (White-eyed Robin) trials were 54% that of conspecific trials (a significant difference between intra- and interspecific aggression), whereas the corresponding values for White-eyed Robins (to Slaty Robin playback) and Black Fantails (to Dimorphic Fantail playback) were 97% and 92%, respectively. Thus, for White-eyed Robins and Black Fantails, there was no significant difference between intra- and interspecific aggression at their leading range margin.

## DISCUSSION

We documented interspecific aggression in three species-pairs of New Guinean songbird elevational replacements that had zones of elevational overlap where both species were present. This finding adds to a growing list of field experiments supporting the hypothesis that interspecific aggression is one mechanism that explains why elevational replacements with zones of overlap where species interact ecologically inhabit largely parapatric elevational distributions (Jankowski et al. 2010, Caro et al. 2013, Pasch et al. 2013). Interspecific aggression was strongly asymmetric in each case—the lower elevation species responded more aggressively to playback of upper elevation species than vice versa (Figures 1 & 2). This result suggests that the lower elevation species in the species-pairs we studied are behaviorally dominant (see also *Catharus* thrushes in Jankowski et al. 2010).

In contrast, we did not find interspecific aggression between two species-pairs that had "no man's land" gaps between their elevational distributions and therefore likely did not directly interact with one another during our field study (Figure 3). This lack of apparent direct interaction appears to have resulted in a qualitatively different response to

heterospecific playback that suggests direct interaction is associated with interspecific aggression. Supporting this hypothesis, interspecific aggression by lower elevation species in this study in the three species-pairs with elevational overlap was always strongest at the lower elevation species' leading range margin (where it interacted with its elevational replacement) and declined downslope from the contact zone (Figures 1 & 2). These declines in aggression occurred over short distances (< 0.5 km), and are most consistent with the possibility that interspecific aggression is a learned response to the presence of a heterospecific competitor (Baker and Lynch 1991, Gil 1997, Sedlacek et al. 2006, Jankowski et al. 2010), the same result found by previous studies of interspecific aggression between songbird elevational replacements (Jankowski et al. 2010, Caro et al. 2013), though we cannot rule out the possibility that interspecific aggression could represent, at least in part, misdirected intraspecific aggression (Murray 1971, Wolfenden et al. 2015) or an evolved response to interspecific interference competition.

We present data consistent with the hypothesis that interspecific aggression influences the elevational limits of species-pairs of New Guinean elevational replacements. Given that elevational replacements comprise roughly 20% of the total avifuana along New Guinean elevational gradients (Freeman et al. 2013, Freeman and Class Freeman 2014b), interspecific aggression could be an important mechanism influencing elevational patterns in this avifauna. Our results are based on a small sample of elevational replacements whose ecological traits (e.g., high relative abundance, known territorial behavior) made experimental song playback tests of interspecific aggression feasible. This will likely be the case for any future examinations of the same hypotheses within a limited geographical area. In adition, it is clear that other factors also limit our

study species' elevational distributions. Most obviously, we did not detect interspecific aggression in two of the species-pairs we investigated (Figure 3). For the species-pairs with interspecific aggression, additional factors must be present that prevent the more aggressive species from continually expanding its distribution.

As global warming drives temperature increases in montane regions, populations of birds (and other taxa) are generally moving upslope (Chen et al. 2011, Freeman and Class Freeman 2014a). Recently, it has been hypothesized that interspecific aggression could influence elevational replacements' upslope shifts; with temperature increases, behaviorally dominant lower elevation species could "push" a subordinate montane species' population upslope at a faster rate than if the lower elevation species was absent, or, if upper elevation species are behaviorally dominant, upper elevation species could maintain their position as "kings of the mountain" (Jankowski et al. 2010). Most species at the study site are shifting upslope at both lower and upper elevational limits (Freeman and Class Freeman 2014a). It is worth noting that the three species that show interspecific aggression towards their upper elevation replacement (White-rumped Robin, White-eyed Robin and Black Fantail) have all expanded their upper elevational limits significanty upslope, while the two species that do not show interspecific aggression to their upper elevation replacement (Chestnut-backed Jewel-babbler and Slaty Robin) have not shifted upslope (Freeman and Class Freeman 2014a). Though highly speculative and based off a small sample size, this observation is consistent with the possibility that interspecific aggression is one factor influencing species' warming-associated upslope shifts at this site. Finally, our results add support to the argument that entire elevational gradients on tropical mountains, the most diverse terrestrial habitats on Earth (Laurance et al. 2011),

need to be treated as a single conservation units. These gradients not only provide the necessary space to accommodate warming-associated upslope shifts for most species, but also serve as irreplaceable working laboratories to investigate abiotic and biotic drivers of distributional limits and community assembly.

**ACKNOWLEDGMENTS**

We thank Karimui residents for their assistance, especially J. Anuabo, S. Banu, J. Buga Tane, W. Paro and D. Goma. The Macaulay Library of Natural Sounds supplied audio recording equipment, and comments from J. Fitzpatrick greatly improved this manuscript. This work was supported by National Geographic Society CRE grant 9117-12 to A.M.C.F. and B.G.F. and by the National Science Foundation Graduate Research Fellowship under Grant No. 2011083591 to B.G.F.

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